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Gregor Mendel

X-Rays in Plant Breeding — *Comb and Crest in Fowls*

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The American Genetic Association

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IN THIS ISSUE

SOME GENETIC EFFECTS OF X-RAYS IN PLANTS
By L. J. Stadler 3

"PARTED PARIETALS" IN MICE
By Clyde E. Keeler 19

THE ASSOCIATION OF COMB AND CREST CHARACTERS IN THE DOMESTIC FOWL
By Morley A. Jull 21

MATRIMONIAL PROSPECTS OF SOUTHERN COLLEGE WOMEN
By Roland M. Harper 29

POLLEN STERILITY IN THE COLLINSON AVACADO
By T. Ralph Robinson 35

ABNORMALITIES IN PECANS
By J. G. Woodroof and Naomi C. Woodroof 39

HERITABLE CHARACTERS IN MAIZE
By George W. Beadle 45

POPULATION OF UNITED STATES NEARLY 120 MILLION 20

AGRICULTURE ON THE HYPOTENUSE (A Review) 28

THE "FUCHSIA-PICTURE" OF MENDEL 33

BOOKS RECEIVED 38

COMING

Identical Triplets

Human "pure lines" come in threes as well as in pairs—some excellent examples.

The Siamese Cat

Interaction of heredity and environment (temperature) in producing coat-color in this cat.

The Porcupine Pigeon

A Mendelian character that turns feathers to quills.

Duck-Legged Cattle

Herefords, except that they are four to six inches nearer the ground—one of the few instances in farm animals of the transfer of a Mendelian character from one breed to another.

Human Chromosome Number

A review of recent research that appears to have settled a moot question.

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X-RAYS IN APPLE BREEDING

Frontispiece

The tree fruits are complex heterozygotes in which breeding methods applicable in the improvement of crop plants produce discouragingly slow results. The work with X-rays suggests that by this means a greatly increased rate of bud mutation may be induced in fruit trees; the chance of successful application of induced mutation in economic plant breeding appears to be greatest in this field.

SOME GENETIC EFFECTS OF X-RAYS IN PLANTS*

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THIS paper summarizes the results of a series of experiments on the genetic effects of X-rays, conducted at the University of Missouri during the last four years. The experimental material has included various plant species, chiefly barley (*Hordeum vulgare*) and maize (*Zea mays*). Space will not permit the detailed presentation of experimental methods or data in this summary, but fuller accounts of the individual experiments have been, or will be, published separately.

Mutation Induced by X-Rays and Radium

The effects of X-ray and radium treatments on the frequency of mutation in barley were determined by the method illustrated in Figure 1. The treatments were applied to dormant or germinating seeds, which were then planted at sufficient distance to permit the development of several tillers. The tillers develop from the axils of the lower leaves, and each terminates, as does the central culm, in a seed-bearing head. Since the primordia of the tillers are separate in the embryo at the time of treatment, a mutation occurring at this time affects only a single culm. (In much-tillered plants a secondary tiller often develops from an earlier tiller, and a single mutation may affect both).

The occurrence of a mutation is detected by growing a self-fertilized progeny from each head. The mutant character segregates in the progeny of a single head, and its absence in the progenies of other heads of the same plant shows that it has resulted from a genetic change occurring during the development of the plant treated. Ancestral hybridity, pollen contamination, or other complications could account for the segregation of an unexpected character in the progeny of a treated plant, but in any such case the character would segregate similarly in all head progenies of the plant concerned.

In the first series of experiments, in which about 2,800 head progenies from X-rayed and radium-treated plants were examined, 53 mutations were found. In the untreated control, including about 1,500 head progenies, no mutations were found. Of the 53 mutations 48 were recognizable in the seedling stage. The methods of treatment and the mutant seedling characters have been reported elsewhere.[4]

Since about 90 per cent of the mutations found could be recognized in the seedling stage, the use of seedling mutations alone as an index to mutation rate is feasible. This permits the determination of mutation rates on a large scale. Each head progeny may be examined for seedling segregation in a planting occupying about 15 square inches for a period of 10 days, and tests may be made in the greenhouse at any season of the year. The occurrence of seedling mutations is, in fact, determined more accurately under these conditions than in the regular field plantings, since the less viable mutant types sometimes fail to emerge under field conditions. Seed remnants of all head progenies are saved and those from mutating plants are planted in the field for further study.

By this method quantitative studies of mutation rate may be made with

*These experiments were supported in part by a grant from the National Research Council, Committee on Effects of Radiation on Living Organisms.

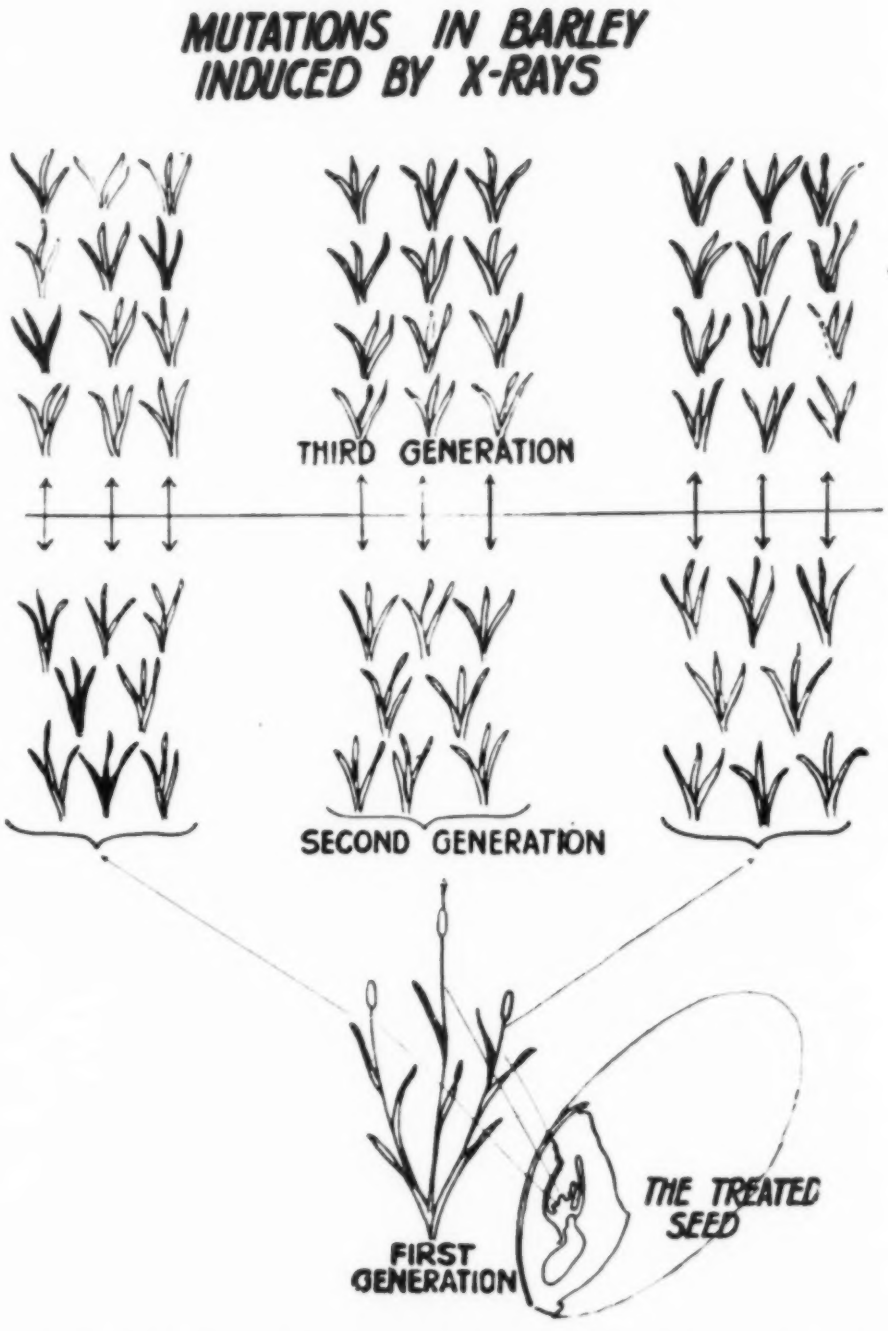
ordinary "visible" mutations. During the fall of 1928 seedling progenies were grown in the greenhouse from about 20,000 head progenies. Only distinct and conspicuous seedling characters were counted as mutants, in order to avoid fluctuation in the standard. About 250 of these were found. The evidence discussed below on the relation of mutation rate to dormancy, temperature. dosage, etc., is derived from these experiments.

The Induced Mutations

The mutant seedling characters recorded were chiefly chlorophyll abnormalities. The predominance of this type of mutant is due in part to the method of study, since special attention was given to characters showing clear-cut segregation in small progenies during the first few days after emergence. This method discriminates against any but the most extreme of morphological variations. A few clear-cut morphological variants, however, are included.

Of the total number of seedling mutants found, some 300 in all, white seedlings made up about 60 per cent. Another 5 per cent were "virescent white"; that is, white seedlings which gradually develop green color. About 15 per cent were yellow seedlings of various shades, of which about one-third were more or less virescent. Intermediate shades of greenish-yellow made up another 10 per cent, and the remaining 10 per cent included miscellaneous types such as "striped", "banded", "fine - striped", "green - striped", "tarnished", "spotted", "tapering", spindling", "shriveled", etc. The mutants grouped as virescent whites, yellows, and greenish-yellows included many phenotypically distinct types. Presumably these as well as the white seedlings included mutations at many different loci.

Most of the mutant seedling characters are lethal and almost all are unfavorable to growth, as would be expected in types conspicuously different from the normal. The striped seedlings are fairly vigorous, and a few



TECHNIC IN DETERMINING MUTATION RATE IN BARLEY

Figure 1

A recessive mutation induced by irradiation of the seed makes one tiller of the resulting plant heterozygous. In the second generation the selfed progeny of this tiller segregates the mutant character. Some of the normal plants of this progeny are heterozygous, and segregate the same mutant in the next generation. Since the primordia of the three heads are separate in the embryo at the time of treatment, the other head progenies of the treated plant are unaffected by the mutation.

of the virescents develop almost normally in later growth.

Mutations having no conspicuous effect in the seedling stage but causing distinct variations in later development could have been detected in only about 4,000 head progenies which have been grown to maturity. Seven of these were found, including three for "pale green," two for "non-glaucous," one for "fine-stripe," and one for "dormant," a type resembling winter barley in habit of growth.

DIRECTLY-INDUCED STRIPING

Figure 2

A barley chimera resulting from a direct cytoplasmic effect of X-ray treatment. The two tillers on the right had broad yellow stripes, but the heads were entirely green. The progeny was unaffected. In a similar plant in which a yellow stripe passed through the head, the seed of the striped sector transmitted the defect.

Tests of almost all of the mutations found in the first series of experiments have been carried through one or more generations following that in which the mutant character first appeared. In all of these cases the head progeny segregating the mutant includes normal plants which segregate the same mutant in the next generation. The few mutants which reach maturity breed true. In the few cases tested by crossing on untreated normal plants, the mutant characters are transmitted through the pollen, reappearing as recessive segregates in the F_2 of the hybrid. In other words, the genetic behavior is as would be expected on the assumption that the mutation is a change of a dominant gene to the corresponding recessive in a somatic cell of a homozygous plant.

In the original segregating head progeny the proportion of plants showing the mutant character is usually less than 25 per cent, and the proportion of plants which are found heterozygous is less than 50 per cent. In later generations the ratios are approximately normal. The probable reason is that only a part of the head is derived from the cell in which the mutation occurred.

Not infrequently two different mutant characters segregate in the same head progeny. The frequency of such cases is greater than would be expected from chance coincidence.

No clear case of a dominant mutation has yet appeared. All of the mutations tested beyond the first segregating generation are unquestionably recessive. The remainder cannot be classified positively without further test, but none of them has behaved as would be expected of dominants. A dominant mutation should affect not only the progeny of the tiller concerned, but also the phenotype of the tiller itself. All of the treated plants, including many not yet tested for recessive mutation, were carefully examined for somatic variations such as might result from the occurrence of dominant mutations in the primordia of tillers. Among more than

CHIMERAS INDUCED BY X-RAYS

Figures 3 and 4

Two maize chimeras resulting from X-ray treatment of the mature seed. Both are purple plants heterozygous for the gene *B b*, and each has a sector of green tissue derived from a cell in which *B* was lost. The extent of such sectors indicates the amount of tissue which may be derived from a single cell in the embryo of the mature seed.

CHIMERAS PRODUCED BY IRRADIATION OF DEVELOPING EMBRYO

Figures 5 and 6

Two maize chimeras resulting from irradiation 6 days after pollination. Both plants were heterozygous for the gene *G g*, for golden plant color. The lighter colored areas in the figure are "golden," and are derived from a cell in which *G* was lost.

23,000 treated plants only two variations affecting seed-bearing culms were found. One of these was the plant pictured in Figure 2. Two of its tillers (on the same side of the plant) had distinct broad yellow stripes on the leaf blades and sheaths but not on the head. The progeny of these two tillers was entirely normal. The other plant had a similar yellow stripe on the upper sheaths and blades of the main stalk, beginning as a narrow line but broadening on the upper leaves and appearing on several spikelets of the head. The seed of these spikelets gave yellow, green, and sectorially yellow-and-green plants. Probably both cases resulted from some direct cytoplasmic effect of the X-ray treatment. A third case was a plant with broad white stripes on two late tillers, which never headed and which therefore could not be genetically tested. No other indication of dominant mutation has been found. From the tests already completed it is evident that the total number of recessive mutations from these plants will be over 1,000.

The possibility is not excluded that the recessive condition resulting from X-ray treatment is merely the absence of the dominant gene; that is, that the mutation induced is simply the destruction of a gene. But the outward effects and genetic behavior of these mutations, so far as studied, are identical with those of "normal" recessive genes, and this conception may be applied equally well to "normal" recessive mutation.

Tests of the genetic identity and linkage relations of several of the induced mutations have been undertaken by Prof. F. J. Stevenson, of the University of Minnesota, in connection with his studies of inheritance in barley. The material is technically rather difficult, and routine determination of the linkage relations of large numbers of mutant genes is not practicable.

Induced Mutation In Maize

In experiments in which detailed genetic study of the induced mutations is desirable, maize is now being used, because of its advantages for genetic analysis. Mutations similar to those found in barley are induced in maize by X-ray treatment. Since maize is naturally cross-pollinated, the treated plants must be self-pollinated artificially, and it is therefore not so well suited as is barley to the determination of mutation rates on the extensive scale necessary in quantitative studies.

The portion of the plant which will be affected by a mutation occurring in a single cell of a mature seed is not likely to include both the tassel and the ear, and consequently the mutations induced by treatment of mature seed usually do not segregate in the second generation. A mutation affecting either the tassel or ear, but not both, results in the production of heterozygous plants in the second generation and segregation in the third. By using only tiller ears and pollinating each with pollen from the same tiller, the chance of a second generation segregation is increased. A more satisfactory method is to apply the treatment not to the mature seed, but to the young embryo, at so early a stage that an induced mutation can affect the entire plant.

The portion of the plant affected by mutations resulting from treatment of the embryo at various stages of development is shown in chimeras produced by the treatment of embryos heterozygous for certain plant characters. The plants shown in figures 3 and 4 are from seeds X-rayed just before planting. They are heterozygous for purple plant color, and each shows a sector of green tissue developed from a cell in which a plant-color gene (B) was lost. The genetic nature of these cases is discussed in a later paragraph. The point of interest in the present connection is the extent of the tissue which may be affected by a genetic change resulting from treatment at this stage of development. Several chimeras of this sort have occurred in cultures grown from X-rayed seed. The affected tis-

ABERRANT PLANTS DUE TO IRRADIATION

Figures 7 and 8

A defective plant from a seed X-rayed at fertilization. The plant at the left is a normal plant of the same culture. Plants are similarly affected by irradiation on the day after fertilization.

A japonica-striped maize plant from the irradiation of an embryo heterozygous for *J j* shortly after fertilization. The entire plant is derived from a cell in which *J* was lost.

sue in these plants varies rather widely in extent. Plant 1252-27, pictured in Figure 3, has the largest portion of tissue affected, while plant 1214-55 (Figure 4) has one of the smallest sectors observed. In the former plant, part of both the tassel and the ear are affected, while in the latter apparently no portion of either the tassel or the ear is included in the affected sector.

Even when treatments are applied as early as the sixth day after pollination chimeras are produced. The plants shown in Figures 5 and 6 were produced in this way. In these two cases the gene responsible is *G g*, for golden plant color. Both plants have broad streaks of goiden tissue in both the main stalk and the tillers. None of the plants from seed treated at this stage showed a recessive character affecting the entire plant. On the other hand, treatments applied on the first or second day after pollination have produced no chimeras, but have given several plants entirely recessive for a character heterozygous in the seed treated. One of these is shown in Figure 8.

In studies of induced mutation in maize the X-ray treatment is applied to seeds heterozygous for genes marking several or all of the chromosomes. These are treated in the field on the second day after pollination. The plants grown from these seeds are selfed. The induced mutations thus segregate in a progeny segregating also for the chromosome markers, and linkage relations are roughly indicated in the generation in which the mutant characters first appear. So far as possible, genes for endosperm and seedling characters are used as chromosome markers, in order to permit the determination of mutation frequency and linkage relations in seedling progenies.

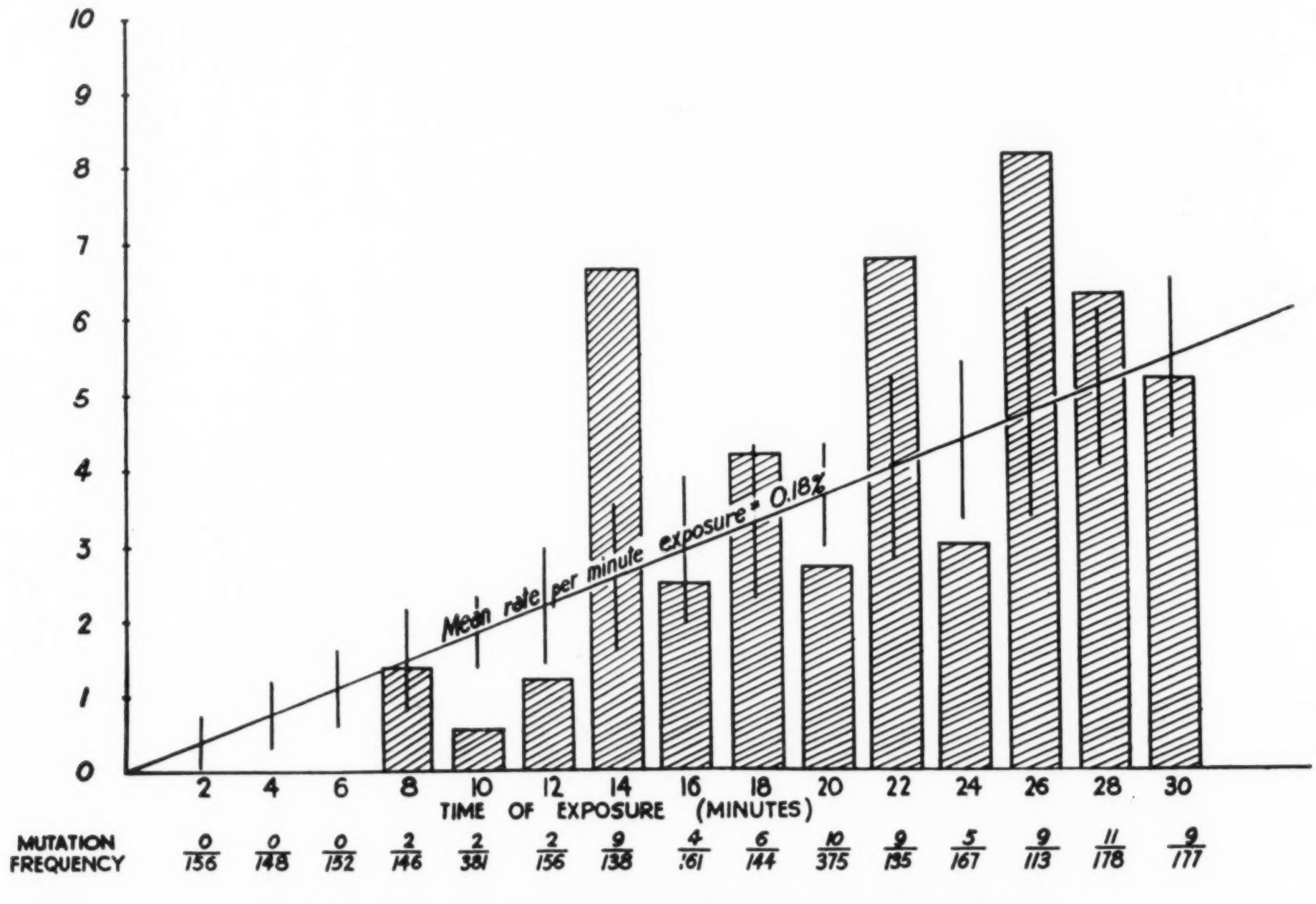
Rarity of Induced Mutation in Wheat and Oats

Treatment of common wheat and oats by the methods described above for barley gives a very different result. The effect on the treated generation is similar, and the killing dose is not markedly different, but in the following generations there is little or no evidence of induced mutation.

Common oats of the two cultivated species, *Avena sativa* and *Avena byzantina* were treated in several experiments. Selections of the varieties Kherson and Fulghum were used. The conditions of treatment varied somewhat in these experiments, but were such as would have yielded about 50 seedling mutations if applied to barley on the same scale. Only one mutation was found in the oats, a white seedling segregation in Kherson oats treated as dormant seed.

Common wheat (*Triticum vulgare*) was treated on a scale which would have yielded about 40 mutations in barley. Harvest Queen, a winter wheat, and Marquis, a spring wheat, were used. No mutations were found.

It is probable that the cause of the lower mutability of oats and wheat is gene reduplication, connected with their higher chromosome number. Each of the genera Hordeum, Avena, and Triticum includes species with chromosome numbers of 7", 14", and 21", but the cultivated barleys belong to the 7" group in Hordeum, while the cultivated oats and wheats belong to the 21" groups in Avena and Triticum. Whether the 21" condition has arisen by simple chromosome reduplication or by some more complex process involving the combination of unlike but related sets of 7", it is probable that most genes would be present in duplicate or triplicate in the haploid complement of 21 chromosomes. If a dominant gene *A* were present in triplicate *AAA*, recessive mutation of one *A* could have no visible effect, for the duplicate dominants would still be present to maintain the dominant condition. The coincidental mutation of the three homologous genes would probably be so rare as to be negligible. A moderate rate of mutation might result from the presence of some genes in the *aaA* condition, as a result of previous mutations occurring in the course of the past evolution of the species.



MUTATION RATE PROPORTIONAL TO DOSAGE

Figure 9

Relation of mutation frequency to dosage. The rate of mutation is proportional to the total intensity of the radiation applied, within the limits of sampling error. Detailed explanation in text.

If this hypothesis is correct the species of Avena and Triticum with 7 pairs of chromosomes should mutate at rates comparable with those of common barley. Tests of these species, as well as some of the 14″ species, are now in progress.*

Mutation Induced in Dormant Tissue

It is well known that the physiological effects of X-rays are in general intensified in actively growing tissue. In attempting to induce mutation by seed treatment with X-rays, experiments were made first with seeds germinating under optimum conditions, and the treatments were applied intermittently in order to increase the number of dividing cells exposed to treatment. But our present fragmentary knowledge of the nature of the gene gives us no reason to assume that the effect of X-rays on mutation would vary with the metabolic activity of the cell. If the gene is a constant entity and its mutation a chemical change energized by radiation, it might reasonably be expected to mutate under irradiation as readily in dormant as in active cells. A consistent difference in the rate of mutation found in cells at different levels of metabolism might serve as a clue to the physical nature of the mutation process.

Dormant and germinating seeds of barley were given identical X-ray

*These tests have been completed and published.

treatments in three experiments.[5] The dose was near the limiting intensity for germinating seed. Dormant seed are much more resistant to injury by irradiation and will withstand 15 to 20 times as heavy a dose.

The average rate of mutation in the plants treated as germinating seeds in these experiments was about four times as high as that in plants treated as dormant seeds. In each case the rate was determined from about 2500 head progenies, and the difference was unquestionably significant from the statistical standpoint. The number of mutations found after irradiation of the dormant seeds was large enough also to indicate positively that mutations were occurring at a rate significantly higher than that in untreated seeds. When the dose applied to dormant seeds was doubled the rate of mutation was approximately doubled also. The double dose applied to germinating seeds was almost completely lethal.

Because of the greater tolerance of the dormant seed, it was possible to apply a dose 10 times the unit dose without appreciable injury to the plants. This resulted in an increase in the mutation rate roughly proportional to the increase in dosage. The mutation rate thus secured was more than double that which followed the irradiation of germinating seeds. In spite of the higher mutability of germinating seeds, it is likely that the maximum sub-lethal dosage of dormant seeds will be much more effective in inducing mutation than that of germinating seeds. Their greater tolerance is more than enough to compensate for their lower rate of mutation.

When seeds which have been irradiated while dormant were stored for two weeks before planting, the percentage of mutations was not appreciably changed. The most heavily irradiated seeds, though apparently uninjured when planted immediately after treatment, decreased greatly in viability during the storage period. In seeds given lighter doses there was no noticeable loss during storage, either in germination or in vigor of growth.

Increased moisture content alone is not responsible for the increased mutability in germinating seeds. The "germinating seeds" referred to above were seeds soaked in water for 6 hours and kept on moist blotters in covered dishes for 18 hours before treatment. When seeds were irradiated immediately after the soaking period the mutation rate was not significantly higher than that in dormant seeds.

By changing the length of the period of soaking, the moisture content of the seed may be widely varied. Identical treatments were applied immediately after soaking to five lots of seed with moisture content of approximately 15, 20, 25, 30, and 40 per cent. The rate of mutation was not appreciably affected.

Temperature of the seeds during irradiation has no pronounced effect on the rate of induced mutation. Germinating seeds irradiated at 10°, 20°, 30°, 40°, and 50° Centigrade showed no significant difference in mutation rate. The limits of sampling error in the experiment admit the possibility of a small effect of temperature, but it is clear that the high temperature coefficient characteristic of many biological reactions does not apply. Similar experiments with dormant seed gave the same result.

Relation of Mutation Frequency to X-Ray Intensity and Wave-Length

The radiation applied in the experiments summarized above varied in both intensity and wave length. In most cases the total intensity applied was well below the tolerance limit of the seed. The wave length range in almost all cases was that of unfiltered radiation at voltages of 54 to 108 K. V. P.

To determine the relation of total intensity to mutation rate, dosage trials were made with both dormant and germinating seeds. Dosage was varied by changing the duration of the

treatment, other factors affecting radiation intensity being constant. (108 K. V.P., 4 m.a. tube current, 18 cm. target distance, no filter).

Fifteen doses were compared in the trial with dormant seed, ranging from 2 to 30 minutes. The heaviest dose had no appreciable effect on the viability of the seed or the vigor of the plants. Later trials showed that a 60-minute exposure under these conditions killed about one-half of the plants.

The frequency of mutation in plants given these treatments is shown in Figure 9. Mutation frequency increased approximately in direct proportion to dosage. Considering all of the data the mean rate of mutation per minute of exposure was 0.18%. This determines the slope of the line in the graph. If mutation rate is proportional to dosage the mutation frequency from any dose should be indicated within the limits of sampling error by the slope of this line. The probable error of the expected mutation percentage for each dose in a population of the size used is indicated by the vertical lines, and the mutation percentages actually found are indicated by the vertical columns. For example, the expected mutation percentage for an exposure of 20 minutes, in a population of 375, is 3.6 ± 0.7; the observed percentage is 2.7. As the graph shows, the actual mutation rates did not deviate from strict proportionality more than might reasonably be expected as a result of sampling fluctuations.

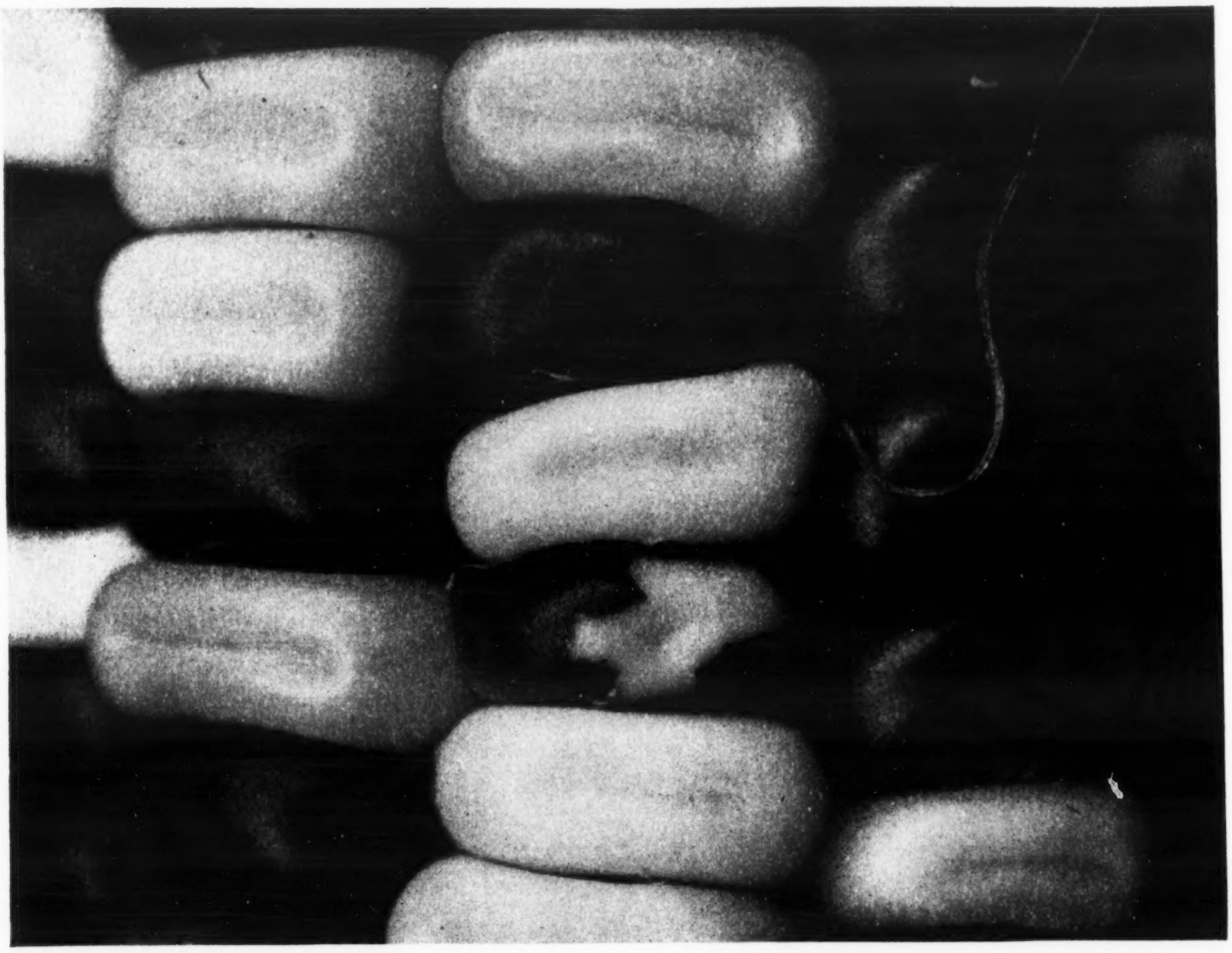
The absence of mutation in the cultures given the three lowest doses might suggest the possibility of a threshold intensity below which mutations do not occur, but in other experiments with low dosage mutations have been found. In the experiments with temperature mentioned above, 1270 progenies from seeds given an exposure of 108 seconds under the same conditions as in the dosage trials yielded 4 mutations, and 1005 progenies from a 216-second treatment yielded 7 mutations. These rates are proportional to those found in the dosage trial.

In the dosage trial with germinating seeds the range in exposure was from 15 to 360 seconds. All exposures above 135 seconds reduced viability, but even at 360 seconds some plants produced seed. The relation of mutation rate to dosage was similar to that found in dormant seed. The mean rate of mutation per minute of exposure was 1.17%, about 6 times that found in dormant seeds.

X-rays through a wide range of wave lengths appear to be about equal in power to cause mutation, when applied in intensities equal in power to ionize air. Equal intensities, as measured by ionization tests, were applied to both dormant and germinating seed of barley at 40, 56, 81, 98, and 116 K.V.P. Mutations were induced by all of the treatments, and the frequency of mutation did not differ significantly. Later, through the kindness of Dr. Gustav Bucky, of New York City, it was possibly to apply accurately measured doses of the ultra-soft X-rays, or "grenz rays," emitted by the Bucky soft X-ray tube. Mutations were induced by this radiation, both at 10 K.V.P. and at 7 K.V.P. At the latter setting no radiation of wave length shorter than 1.76 Å. is included in the emission spectrum.

Effects of X-Rays on Chromosome Distribution

In quantitative studies of the chromosomal effects of X-ray treatments the material chiefly used was mosaic endosperm of maize. A mosaic endosperm is an endosperm chimera in which a portion differs from the remainder in one or more characters, due to a genetic change occurring in early development. Emerson has shown that the phenomenon is due, in most cases at least, to a chromosomal disturbance, since linked genes are usually lost together, while unlinked genes are not. Since the triploid endosperm nucleus contains two identical sets of chromo-



ENDOSPERM CHIMERA DUE TO CHROMOSOME IRREGULARITY

Figure 10

Mosaic endosperm in maize produced by irradiation. In a seed heterozygous for the linked genes *C*, *Sh*, and *Wx*, a sector comprising one-fourth of the endosperm has lost the three dominant genes, and is colorless, shrunken and waxy (*c sh wx*). The cause is a chromosomal irregularly in early endosperm development.

somes from the female parent, the loss of a dominant gene of maternal origin has no visible effect. Mosaics occur only for characters recessive in the female parent and dominant in the male. The cytological nature of the chromosome aberration causing mosaic endosperm is unknown.

Figure 10 illustrates mosaic endosperm in a grain heterozygous for the linked genes *C c*, *Sh sh*, and *Wx wx*. About one-fourth of the grain is colorless, shrunken and waxy (*c sh wx*) while the remainder is colored, smooth, and starchy (*C Sh Wx*). At an early stage in endosperm development a chromosome or portion of a chromosome carrying the three dominant genes was lost or inactivated, and the tissue derived from the cell affected lacks the three characters dependent on the lost genes.

Seven of the 10 maize chromosomes carry genes permitting their identification in endosperm mosaics, but the *C-Sh-Wx* chromosome is the only one with more than one gene suitable for accurate work with mosaic endosperm. Mosaics of each of the 7 chromosomes have been observed in untreated material. Their frequency varies rather widely in different families grown under comparable conditions. There is also wide variation in the frequency of mosaics for different characters in the same ears For example, in 9 unrelated families of *A C r su*, the average frequency of *r* mosaics was 0.59%, and that of *su* mosaics 0.05%. If the mosaics are due to losses of an entire

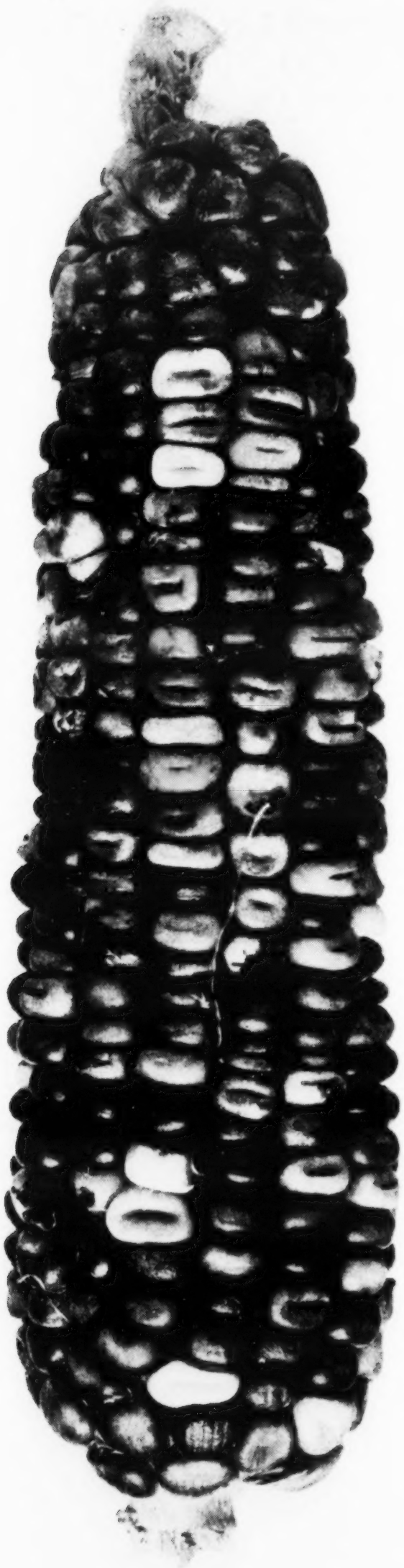


Figure 11

High frequency of mosaic endosperm in an ear X-rayed at the time of fertilization.

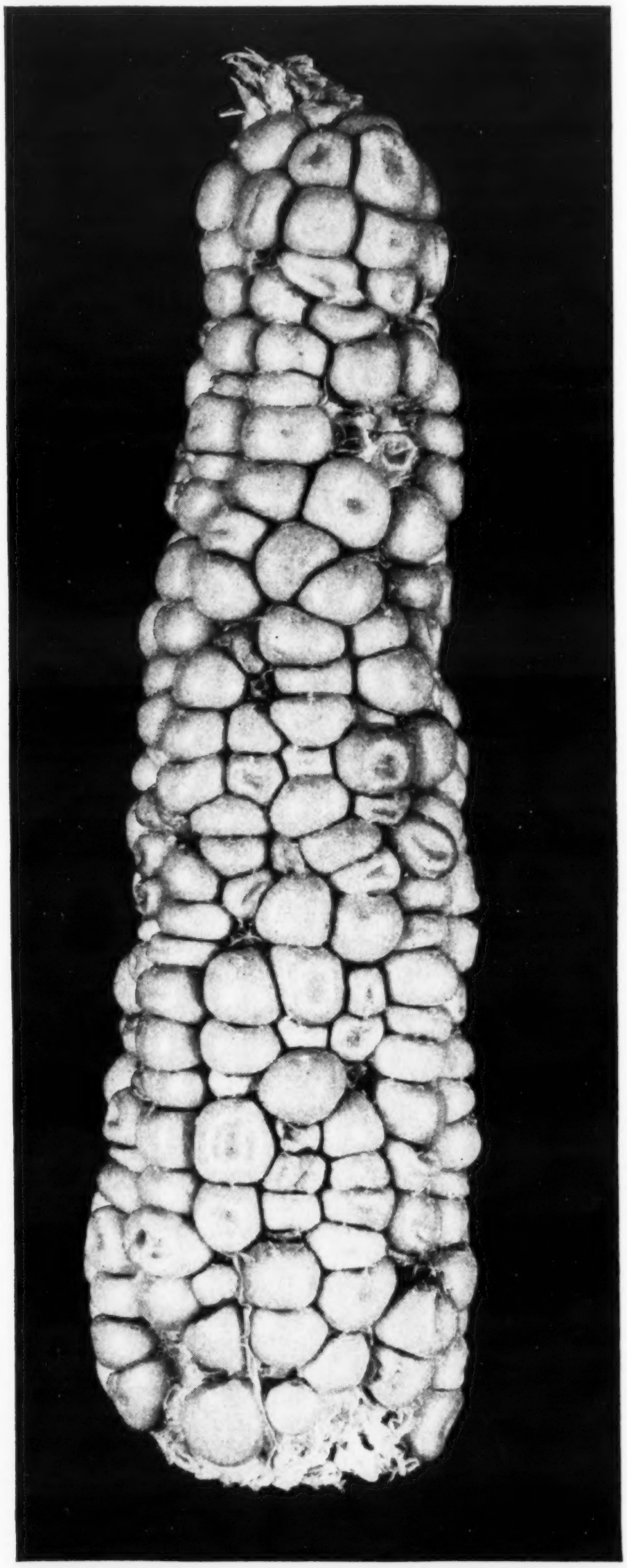


Figure 12

Defective seeds from X-rayed pollen. Many of these seeds are germless. The seed parent was untreated.

MOSAIC AND DEFECTIVE SEEDS

chromosome, this difference would indicate that one chromosome is lost much more readily than another. It seems likely, however, that mosaics are caused, in some cases if not in all, by the loss of only part of the chromosome. In material heterozygous for *C c* and *Wx wx*, the majority of colorless mosaics are waxy, but sectors in which *C* has been lost without *Wx* are not uncommon, either in X-rayed or untreated material.

When an ear is X-rayed at about the time of fertilization a great increase in the frequency of mosaics occurs. Data have previously been published[3] showing a twentyfold increase in the mosaic rate, and larger increases occurred in some later experiments. The ear shown in Figure 11 illustrates the high frequency of mosaics in X-rayed ears. This ear was produced by the cross *A A R R c c sh sh wx wx pr pr Su su* × *A A R R C C Sh Sh Wx Wx Pr Pr Su Su*. Mosaics can show only for the paternal *C-Sh-Wx* and *Pr* chromosomes and in half of the grains for the paternal *Su* chromosome. If the 30 chromosomes present are being lost with an average frequency equal to that of these three, the frequency of chromosome loss was 12 times the frequency of the mosaics on this ear.

In X-rayed ears with numerous mosaics, aberrations involving unlinked genes are occasionally found. In the ear shown in Figure 11 two grains appear which are partly colorless-starchy and partly colored-sugary. Each of these resulted from a cell division in which one of the daughter cells lost *C* while the other lost *Su*. The frequency of such cases is probably no higher than would result from chance coincidence, though more extensive data would be desirable on this point.

When treatment is delayed until the day after fertilization, the mosaic spots showing recessive characters are smaller and more numerous. When the same treatment is applied on the fifth day after fertilization, they are so small and numerous that the seeds appear stippled and the individual spots cannot be distinguished without magnification. Treatments applied two weeks after fertilization have no visible effect on the endosperm.

These treatments cause chromosome irregularities in the young embryo as well as in the young endosperm, as is evidenced in plants grown from seed of the X-rayed ears. Among these there occur (1) plants normal in appearance but with approximately 50 per cent defective pollen, (2) distinctly defective plants, and (3) plants showing recessive characters for which the seeds treated were heterozygous.

(1) Apparently normal plants with partially defective pollen are very frequent in these cultures. Usually about one-half of the pollen is defective. In most of the plants the defective pollen grains are empty, but in some they are partly filled with starch. In almost all cases the ovules of these plants are also partially defective, producing about one-half of a full set of seed distributed at random over the ear. The affected plant, whether self-fertilized or crossed with a normal plant, yields a progeny of which about 50 per cent are similarly affected. Brink and Burnham[1] have analyzed a similar case occurring in untreated maize. From the genetic evidence they ascribe the phenomenon to chromosomal translocation. It is interesting in this connection that Muller and Painter[2] have found translocation common in X-rayed Drosophila.

(2) The defective plants are of various types, but are all distinctly inferior to the normal plants in vigor of growth. Some never reach the flowering stage. Those which do produce partially defective pollen and few seeds. One of the more vigorous of these plants is shown in Figure 7 in comparison with a normal plant of the same progeny.

(3) In cultures heterozygous for certain characters a few defective plants showing the recessive character have been found. The japonica-striped plant shown in Figure 8 was one of these. When treatment is delayed sectorial chimeras showing the recessive character in a portion of the plant are pro-

DEFECTIVE PLANT FROM X-RAYED POLLEN

Figure 13

A typical defective plant from seed of a normal plant pollinated by X-rayed pollen. The plant on the left is a normal plant of the same culture.

duced, as shown in Figures 3-6. The pollen in affected plants or sectors is partially defective. These plants apparently represent the loss or inactivation of a chromosome or section carrying the dominant allelomorph of the character involved. Some characters are much more frequently lost in this manner than others.

By a study of the chromosome complement of plants of this sort it may be possible to identify the visible chromosomes with specific linkage groups in maize. The induction of chimeras by X-ray treatment at various stages of development will be a useful method for the study of the developmental morphology of the plant.

Dr. L. F. Randolph has undertaken a cytological study of the effects of these treatments, and has found cytological evidence of a chromosomal irregularity associated with semi-sterility and of chromosomal or sectional deficiency in many of the defective plants.

Chromosomal effects of X-rays are shown also in the results of pollen treatments. An ear of an untreated plant pollinated with heavily-treated pollen is shown in Figure 12. A considerable proportion of the seeds are distinctly defective. Many of these are germless. The viable seeds yield both normal and defective plants. A typical defective plant from treated pollen is shown in comparison with a normal plant of the same progeny in Figure 13. Among the defective plants produced by the use of X-rayed pollen Dr. Randolph has found several lacking an entire chromosome and others lacking a portion of a chromosome. Experiments designed to identify genetically the chromosomes eliminated are now in progress.

Induced Mutation in Plant Breeding

The practical value of induced mutation in the improvement of crop plants has been much overrated, at least as regards immediate application. It is true that progress in plant breeding is dependent on the occurrence of germinal variation, and that the rapidity of germinal change may be greatly increased by X-ray treatment. But it

does not follow that increasing the frequency of mutation a hundredfold will expedite the progress of plant improvement in proportion. In spite of the rarity of mutation under natural conditions, a great wealth of germinal variation is now available in every crop plant species. This is the result of the natural mutation of the past, on so vast a scale as to dwarf the most elaborate experiment. The genes which have survived in the varieties of today are those which have stood the rigorous test of natural selection. All of these are available to the breeder. By hybridization according to principles now well understood, they may be brought into almost any desired combination.

The variations resulting from induced mutation are in most cases unfavorable. Probably this is true of mutations occurring naturally as well, and it is reasonable to expect that among artificially induced mutations a small proportion of favorable variations will be found. But the rare favorable mutation is likely to be accompanied by unfavorable mutations induced by the same treatment. The result is a plant heterozygous for several genes, mostly undesirable. From this heterozygote a desirable combination may be extracted, but in most cases a heterozygote of greater promise could be produced by well-directed hybridization.

If the mutations induced by X-rays are qualitatively identical with those occurring naturally, there is little chance of producing experimentally variations which have not already occurred in nature. Characters of value in breeding are more likely to be found in the varietal collection than in the progeny of X-rayed plants, and here they will occur without the many undesirable gene mutations and chromosome aberrations characteristic of the X-ray progenies. If mutations could be induced selectively the outlook for practical application would be much brighter, but the evidence thus far gives no indication of selective action. A more thorough study of this possibility is needed.

There are, however, certain special cases in which induced mutation, even in the present state of knowledge, offers a fair possibility of successful application. These are in general cases in which hybridization is not feasible or in which a character dependent on a single gene-change is particularly important. Two examples will serve for illustration.

Modern corn breeding employs almost exclusively the technic of "selection in self-fertilized lines". By continuous selection through several generations of inbreeding, as much as possible of the best germ-plasm is concentrated in a few inbred strains, which are later to be used in the production of vigorous first-generation hybrids. Of the thousands of inbred strains which have been produced in this way, a few represent extremely valuable gene-complexes. Their further improvement is difficult, for as inbreeding proceeds they approach complete homozygosity and offer little opportunity for selection. If new variation could be introduced by induced mutation, even though most of the variations were unfavorable, some further improvement by selection might be possible. In cooperation with Dr. J. R. Holbert and Dr. J. G. Dickson, of the United States Department of Agriculture, a study is now being made of the effects of induced mutation on variability in two exceptionally good inbred strains of corn.

Another promising application of induced mutation is in the breeding of the tree fruits. The established fruit varieties are complex heterozygotes maintained by vegetative propagation. Most of them originated as chance seedlings of unknown parentage. Under seed propagation the type is lost at once. For this reason and because of the long reproductive cycle, controlled hybridization is under a great disadvantage in the breeding of these plants. The selection of bud variations is a much simpler method of improvement, for a desirable variation may be propagated at once by grafting. A few important varieties have originated in this

way, but somatic mutation is too rare in most fruit species to provide material for the systematic application of this method. Some of the characters determining fruit quality are known to be dependent on single gene-differences, and it seems not unlikely that induced mutations may result in bud variations of breeding value. In cooperation with Dr. A. E. Murneek, of the University of Missouri, a study is being made of the effects of X-ray treatment on bud variations in the apple.

Literature Cited

1. Brink, R. A. and C. R. Burnham. Inheritance of semi-sterility in maize. *Am. Nat.*, 63, pp. 301-316. 1929.
2. Muller, H. J. and T. S. Painter. The cytological expression of changes in gene alignment produced by X-rays in Drosophila. *Am. Nat.*, 63, pp. 193-200. 1929.
3. Stadler, L. J. Genetic effects of X-rays in maize. *Proc. Nat. Acad. Sciences*, 14, pp. 69175. 1928.
4. ———. Mutations in barley induced by X-rays and radium. *Science*, 68, pp. 186-187. 1928.
5. ———. The rate of induced mutation in relation to dormancy, temperature, and dosage. *Anat. Rec.*, 41, pp. 97. 1928.
6. ———. Chromosome number and the mutation rate in Avena and Triticum. *Proc. Nat. Acad. Sci.*, 15:876-881. 1929.

"PARTED PARIETALS" IN MICE

A Dominant Hereditary Character of the House Mouse, *Mus musculus*

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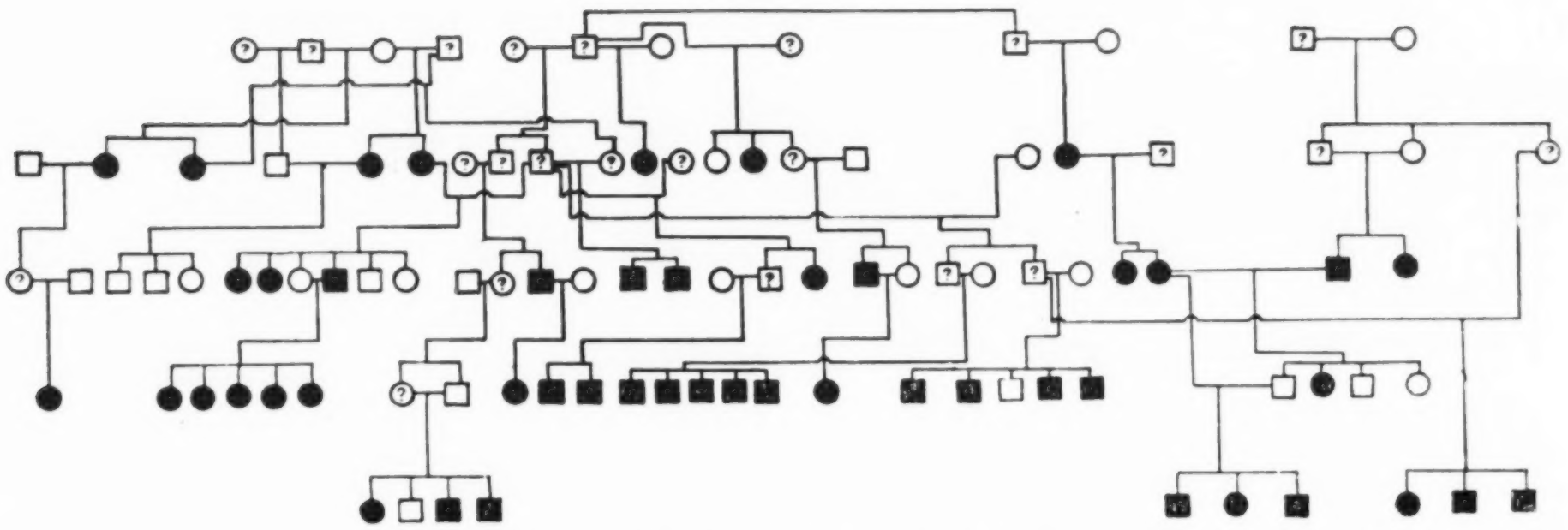
IN the year 1924 many skulls of house mice from different laboratory stocks were collected and cleaned for studies of cranial differences existing between distinct strains and also for investigation of the asymmetry caused by early removal of one eye (unpublished results).

It was discovered that in many mice belonging to my redless strain the median suture separating the parietal bones was spread apart in an unusual fashion (Figure 14). This cranial variation seems to be associated with the presence of a blood vessel, pierc-

"PARTED PARIETALS" AND NORMAL

Figure 14

At left is a skull with "parted parietal," an aperture in the median suture, between the eyes, through which a blood vessel passes. In the normal mouse skull (right) the aperture and the blood vessel are lacking.



INHERITANCE OF PARTED PARIETALS

Figure 15

Chart showing relationships of 100 individuals. "Parted parietals" appears to be a simple dominant to normal skull.

ing the skull at an angle, passes to the exterior between these bones. In other individuals both spread suture and vessel are lacking.

Matings had been made both among these rodless mice *inter se* and also with unrelated mice lacking the "parted parietals." The skulls from offspring of several generations following these crosses were cleaned and examined. From the data in hand a pedigree chart has been prepared (Figure 15) showing the genetic relationship and inheritance of "parted parietals" among one hundred individuals.

In Figure 15 squares represent males, circles females. Blackened symbols indicate affected mice. Normals are represented by hollow symbols. Hollow symbols bearing question marks denote individuals the skulls of which have not been examined.

"Parted parietals" is not associated with sex because the trait appears with equal frequency in both sexes. It is apparently inherited as a dominant unit character because (1) offspring of two affected parents are not all affected, (2) offspring of an affected parent and a normal of unrelated strain not bearing "parted parietals" may be all affected, some affected, or none affected. Only the last-named condition would be compatible with behavior as a recessive character.

Population of U. S. Nearly 120 Million

THE population of the continental United States, as of July 1, 1928, according to the estimate of the National Bureau of Economic Research, made public through the release of advance figures taken from a copyrighted statement issued by the National Bureau, was 119,306,000, or a growth since the same date ten years ago of 14,299,000.

These figures are embodied in a 500-page report which the National Bureau will publish within a few days, entitled The National Income and Its Purchasing Power, and are revealed in a comprehensive tabulation of the number of persons in this country who are gainfully employed, making those who earn money in the form of salaries or wages, or those whose incomes are derived from the conduct of enterprises which they personally control.

THE ASSOCIATION OF COMB AND CREST CHARACTERS IN THE DOMESTIC FOWL

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Senior Poultry Husbandman, U. S. Department of Agriculture

SEVERAL investigators, in crosses involving the Silkie and other breeds of domestic fowls, have observed a peculiar form of rose comb associated with the development of a crest. The peculiarity in the form of the rose comb consists in its relative bluntness posteriorly and in the presence of two or more points in contrast to a single posterior spike, characteristic of normal rose combs in such breeds as Rose-Comb Leghorns, Hamburgs, and Wyandottes. The F_2 progeny from the matings mentioned above for the most part may be divided into two groups, crested birds with rose combs having multiple points and noncrested birds with rose combs having a spike.

Such an association between comb and the presence of crest was observed by Cunningham[3] and Bonhote.[2] The shortening or truncated condition of the comb was suggested by Punnett[6] to be due to the presence of the crest and the multiple-point condition due to a modifying factor. More recently, Dunn and Jull[4] observed that in the F_2 progeny from Silkie×Single-Comb White Leghorn matings nearly all of the rose-comb, noncrested birds had normal shaped rose combs with the characteristic spike. A few exceptions, however, made it doubtful whether the association was complete. Consequently, it became necessary to determine whether the association is due to linkage, organic correlation, or to two effects of the same gene. Further matings to determine which of the three alternatives produces the result were undertaken at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland. The results of these matings are reported in this paper.

The different types of combs involved in this study of the association of comb and crest characters include the Silkie type of rose comb, the type of rose comb normally found in the rose comb Leghorn varieties, the type of single comb normally found in single-comb Leghorn varieties and in Plymouth Rocks, the type of single comb with a distinct lop, and the type of single comb with side-sprigs.

The Silkie type of rose comb is distinctly different from the type of rose comb in rose-comb Leghorns. Dunn[4] described the Silkie type of comb as follows:

> The comb of the Silkie is fleshier in the anterior parts, is shorter, and ends rather bluntly posteriorly in two or more points or papillae, whereas the ordinary rose comb is longer and is characterized by a single long posterior spike or point. Bateson (1909) describes the silkie comb as rose plus trifid element, but I am inclined to agree with Cunningham (1912) that the more important characteristic of the Silkie comb is its abbreviation and bluntness, the more so since it is not regularly trifid but may show from two to four or occasionally more posterior points.

The type of rose comb in rose-comb Leghorns is rather small and relatively slender from front to rear, is covered with numerous small papillae and ends in a prominent spike. (See Figure 16, *D*.)

The type of single comb as found in single-comb Leghorns and in Plymouth Rocks has a base surmounted by well-defined serrations and there is a blade at the rear of the comb. (See Figure 17, *L*.) When a crest is present the single comb frequently is lopped to one side. (See Figure 16, *G* and Figure 17, *K*.) In other cases when a crest is preesnt the single comb has side-sprigs, usually at the rear of the comb. (See Figure 16, *I* and Figure 17, *J*.)

Since there are several types of

combs involved, it seems desirable to adopt a simple terminology to provide for a ready description and classification of the various types of combs in their relation to the presence or absence of a crest. With this in mind terms have been adopted which are self-explanatory. Rose combs with a single posterior spike are called spiked-rose; those with two or more posterior points are called multiple-rose. Single combs are classified according to whether they are lopped or have side-sprigs or are both lopped and have side-sprigs. The terms crested and noncrested are used to denote, respectively, the presence of absence of a crest.

The complete results of all matings are given in Table 1.

The spiked-rose comb, noncrested male used in matings *A*, *B*, and *C* is an extracted type inasmuch as he was out of a White Plymouth female mated to a hybrid male out of a mating between a Silkie male and White Leghorn female. The matings used to produce the male used in matings *A*, *B*, and *C*, are illustrated thus:

Silkie ♂ *R R Cr Cr* × *Leghorn* ♀ *r r cr cr*

F_1 *R r Cr cr*

Back-cross—*R r Cr cr* × White Pl. Rock ♀ *r r cr cr*
Progeny—1 *R r Cr cr*:1 *R r cr cr*:1 *r r Cr cr*:1 *r r cr cr*
The male used in Mating *A* belonged to the *R r cr cr* class

Mating A

Spiked-rose, noncrested ♂ × Spiked-rose, noncrested ♀
R r cr cr × *R r cr cr*

Progeny expected—	3	*R cr*:	1	*r cr*
Progeny observed—97		:17		

In this mating one male was described as multiple-rose, noncrested (see Table 1), but was probably a spiked-rose noncrested, as were all the other rose-comb birds.

The ratio of 97:17 is considerably out of proportion to a 3:1 ratio expected. Upon examination of the progeny of the individual matings it is found that female No. 868 produced 23 rose combs, and no single combs in 1927, and 15 rose combs and no single combs in 1928. All other females produced both rose and single combs. Female No. 868 was obviously homozygous for rose comb. Subtracting the 38 rose combs produced by No. 868 from the total of 97, leaves 59 rose combs produced by the male and females, all of which were heterozygous for rose comb. A proportion of 59:17 approximates the expected ratio of 3:1.

The results of this mating show that the extracted type of rose-comb breeds true *inter se*, which makes it appear that the Silkie type of comb and the crest are produced by a common gene.

Mating B

Spiked-rose, noncrested ♂ × single, noncrested ♀
R r cr cr × *r r cr cr*

Progeny expected—	1	*R cr*:	1	*r cr*
Progeny observed—83		:48		

In this mating the 83 *R cr* birds were all of the spiked-rose, noncrested type, while the 48 *r cr* were all free from side-sprigs. There were 4 birds classified as multiple-rose, noncrested (see Table 1), but this was apparently an error, because spiked-rose combs only are to be expected among the rose combs, judging by the results secured in matings *A* and *C*. Just why there should be such a high proportion of rose-comb birds in mating *B* is unex-

plained, because upon examination of the individual matings it is observed all of the females were heterozygous for rose comb, with the possible exception of one female that produced only one rose-comb progeny.

In matings *A* and *B*, in a total population of 250 birds, there were but 5 apparent exceptions, which were probably spiked-rose, noncrested instead of multiple-rose, noncrested as designated. No spiked-rose, crested birds appeared, so that there is almost complete correlation between the presence of crest and the multiple-point condition of the rose comb. The results in these matings show that the extracted rose comb is of the usual type of rose comb in the absence of a crest. The Silkie fowl, therefore, has the gene for spiked-rose comb as found in rose-comb Leghorns

TABLE I—Showing the results to test the evidence of association between comb form and presence or absence of crest

Mating No.	Sire	Dams	Spiked-rose non-crested	Spiked-rose crested	Mult.-rose non-crested	Mult.-rose crested	Single non-crested	Single crested	Year
A	Spiked-rose non-crested	Spiked-rose non-crested	48	0	1*	0	7	0	1927
			49	0	0	0	10	0	1928
		Total	97	0	1*	0	17	0	
B	" "	Single non-crested	83	0	4*	0	48	0	1928
C	" "	Single crested	36	2†	2**	45	44	33	1927
	" "	" "	24	0	0	32	33	29	1928
		Total	60	2†	2**	77	77	62	
D	Mult.-rose crested	Spiked-rose non-crested	80	0	3**	91	33	27	1927
E	"	Single non-crested	24	0	0	21	14	10	1927

*Probably spiked-rose, noncrested.

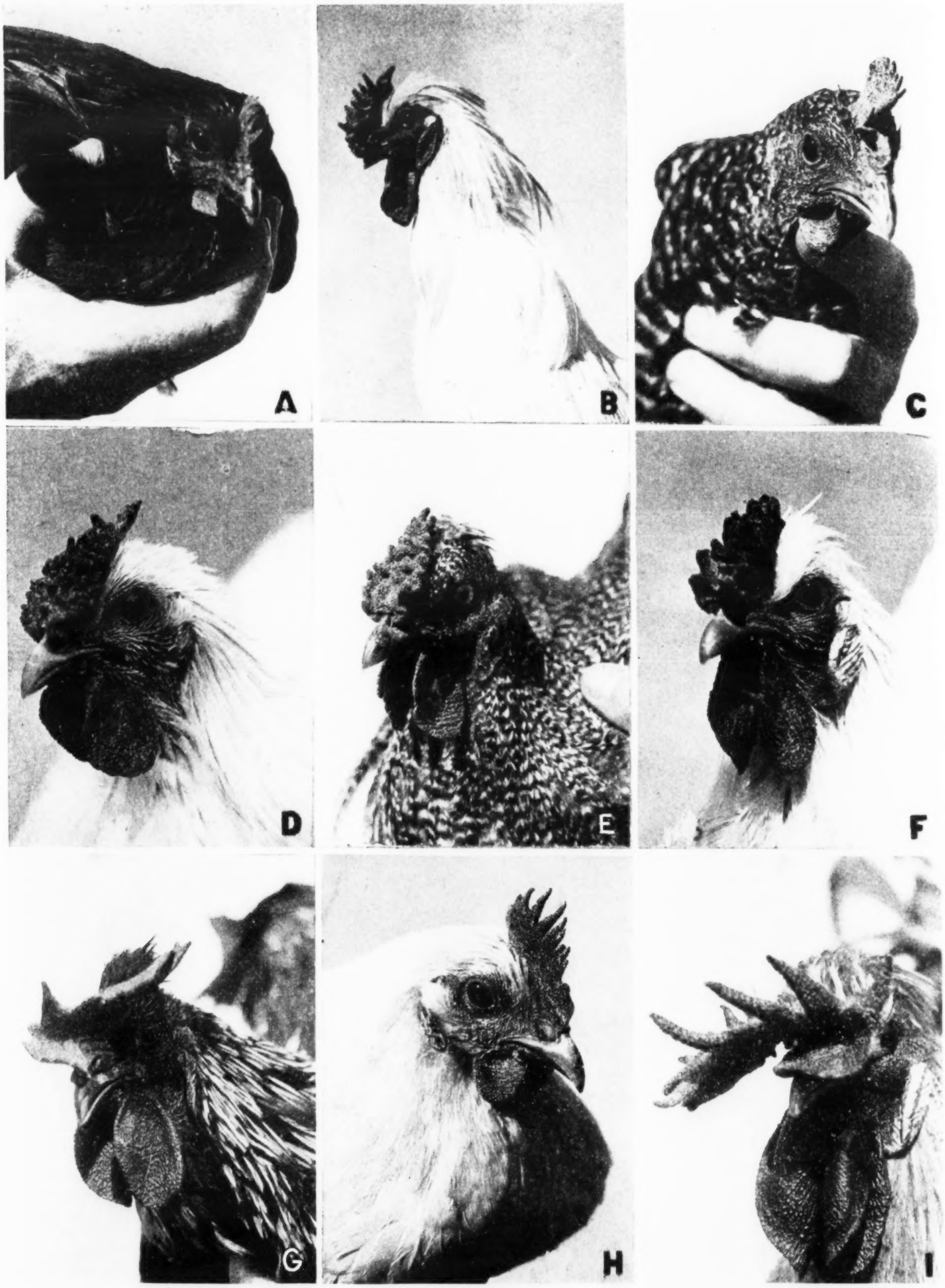
**Probably multiple-rose, crested.

†Probably spiked-rose noncrested or multiple-rose, crested.

Occasionally a bird was encountered whose type of comb it was rather difficult to place. For instance, there were rose-comb birds that seemed to have a spike and additional points as well as a crest and thus at first glance might be classified as spiked-rose, crested. The critical point of determination, however, is the fact that in the presence of a crest the shape of the rose comb is different from that found in Rose-Comb Brown Leghorns. See Fig. 16, *F*. There were other cases even more difficult to classify: those apparently without crests but with two or more points at the rear of the comb, none of which could apparently be designated as a spike. There were 12 apparent exceptions to expectations as shown in Table 1, and these were disposed of before their reexamination was possible. In view of the relatively small number of exceptions it seems probable that the 2 birds in mating C designated as "spiked-rose, crested" were spiked-rose, noncrested and that the other 10 exceptions in matings A, B, C, and D designated as "Multiple-rose, noncrested" were multiple-rose, crested or spiked-rose, noncrested.

In those cases where similar matings were made both in 1927 and 1928, the results for each year are given separately for the sake of comparison. The results are discussed under the heading of each mating Since rose is dominant to single and since crested is dominant to noncrested the respective symbols used are: *R*=rose, *r*=single, *C*=crested, and *cr*=noncrested.

Male No. 8976 was used in matings A, B, and C, and male No. 8973 was used in matings D. and E.



COMB AND CREST TYPES

Figure 16

A, single, noncrested female; *B*, multiple-rose, crested (Male No. 8973 in context); *C*, wrinkled-single, noncrested female; *D*, spiked-rose, noncrested (Male No. 8976 in context); *E*, and *F*, multiple-rose, crested males; *G*, wrinkled-single, crested male; the comb being without sidesprigs; *H*, single, noncrested male; *I*, wrinkled-single, crested male, the comb having sidesprigs. The presence of the crest produces a peculiar type of rose comb, with multiple spikes, instead of a single spike, at the posterior end.

PARENT AND PROGENY IN CRESTED-NONCRESTED MATING

Figure 17

K, wrinkled-single, crested, the comb having sidesprigs (male used in Mating *F* mated to Rhode Island Red females with single combs and noncrested). Others in this figure are the progeny of this mating. *J*, *P*, and *Q*, wrinkled, crested males, the first two having sidesprigs, the last one none; *L*, and *N*, straight, noncrested male and female, respectively; *M* and *O*, wrinkled-crested females; *R*, wrinkled, noncrested male.

Mating C

Spiked-rose, noncrested ♂ × single, crested ♀

R r cr cr × *r r Cr cr*

Progeny expected— 1 *R Cr*: 1 *R cr*: 1 *r Cr*: 1 *r cr*

Progeny observed—77 :60 :62 :77

The 77 *R Cr* birds all had multiple points characteristic of the Silkie comb, while the 60 *R cr* birds all had the single spike characteristic of the Rose-Comb Brown Leghorn, except that 11 of them possessed side-sprigs.

In this mating in a total of 280 birds there were 4 apparent exceptions, 2 classified as "spiked-rose, crested," and 2 as "multiple-rose, noncrested," though these probably represent errors in description as explained in Table 1. Additional evidence in support of the suggestion that the apparent exceptions were wrongly described is that in the 1928 mating there were no exceptions. Also in 1928 the progeny of all matings made that year were gone over carefully for the purpose of selecting birds to be photographed in order to show all types of comb and crest development and no spiked-rose, crested or multiple-rose, noncrested birds were observed.

The results of mating *C* show that whenever rose type of comb and crest occur together, even when rose is introduced by one parent and crest by the other, probably all rose-comb, crested progeny have multiple points and probably all rose-comb, noncrested progeny have spikes.

Mating D

Multiple-rose, crested ♂ × spiked-rose, noncrested ♀

R r Cr cr × *R r cr cr*

Progeny expected— 3 *R Cr*: 1 *r Cr*: 1 *r cr*: 3 *R cr*

Progeny observed—91 :27 :33 :80

There were 3 possible exceptions (see Table 1), but as in other cases the individuals had been disposed of before they could be reexamined. Here again there was no evidence of spiked-rose comb birds having crests, since all 91 *R Cr* birds were multiple-rose, crested and the 80 *R cr* were all spiked-rose, noncrested.

Mating E

Multiple-rose, crested ♂ × single, noncrested ♀

R r Cr cr × *r r cr cr*

Progeny expected— 1 *R Cr*: 1 *r Cr*: 1 *r cr*: 1 *R cr*

Progeny observed—21 :10 :14 :24

The 21 *R Cr* birds were all multiple-rose, crested; the 24 *R cr* birds were all spiked-rose, noncrested, although 2 had side-sprigs. Among the crested birds there were 21 rose to 10 single combs, and among the noncrested birds there were 24 rose to 14 single combs or among all of the progeny there were 45 rose to 24 single combs. The deficiency of single combs has not been satisfactorily explained, although Dunn reports a similar result in some of his matings.

The results of matings *D* and *E* show that when multiple-rose, crested is mated to spiked-rose, noncrested and single, noncrested probably all rose-crested progeny have multiple points and all rose-noncrested progeny have spikes. The three apparent exceptions recorded in Mating *D* (see Table 1) were in all probability errors in observation, particularly when it is realized that no spiked-rose, crested birds were observed in either Mating *D* or *E* and no multiple-rose, noncrested birds in Mating *E*.

Insofar as the relation of crest to multiple-rose comb is concerned, the results of Matings *A* to *E*, inclusive, seem to justify the assumption that the gene for crest acts as a modifier of comb form. In the case of each mating there is almost complete association between the occurrence of crest and the multiple-point condition of the rose comb.

The association between crest and the multiple-point condition cannot be due to linkage because there are no cross-over classes, or at least few exceptions to complete association between crest and the multiple-point condition are practically all of one class.

Regarding the suggestion by Bonhote[2] and Cunningham[3] that the association between crest and the shortened condition is due to the mechanical effect of crest, it may be pointed out, as observed by Dunn and Jull[4] that the muiltiple-point condition of the comb is discernible at hatching time, but the crest does not differentiate until the definitive plumage is developed. Moreover, if the association were due entirely to mechanical effect it might be supposed that the more abundant the crest, the shorter the comb, which, however, has not been observed in the progeny of the matings discussed in this paper.

The general conclusion would seem justified, therefore, that the association between crest and the multiple-point condition of the rose comb is due to the effects of the same gene, the gene for crest acting as a modifier of comb form. The spiked-rose comb of the Leghorn becomes a shortened, multiple-point comb in the presence of a crest, as in the Silkie.

The matings reported in this paper were not made with a view of testing the effect of the gene for crest on single comb, but the observations made show that in the presence of crest, single combs are frequently lopped to one side and that in cases there are side-sprigs on the blades. (See Figures 16 and 17.)

In Mating *C*, of the 62 *r Cr* birds, 7 had side-sprigs, while of the 77 *r cr* birds only 2 had side-sprigs. In Mating *D*, among the 27 *r Cr* birds there were 11 males with side-sprigs, while among the 33 *r cr* birds none had side-sprigs. In Mating *E*, among the 10 *r Cr* birds one had side-sprigs, while none of the 14 *r cr* had side-sprigs. These results make it apparent that the presence of a crest may be associated more frequently with side-sprigs than not.

Though detailed descriptions were not made concerning the lopped or straight condition of single combs when accompanied by a crest, it was observed that the majority of the combs in the males were lopped, as shown in Figure 16 *G* and *I* and Figure 17 *K*, *P*, and *Q*.

Among matings to determine the relationship between rose comb and the presence of crest, Dunn and Jull[4] secured the following results:*

In the back-cross matings the original combination of characters was rose-crested and single-noncrested. In the table below it is observed that in the back-cross matings there is an excess of both rose-crested and single-non-crested. The general conclusion was that the genes for rose comb and for crest are probably loosely linked.

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*Results of Dunn and Jull.

	Rose, Crested	*Rose, Noncrested*	*Single, Crested*	*Single, Noncrested*
F_2 observed	39	12	7	4
F_2 expected	34.9	11.6	11.6	3.9
Back-cross observed	55	39	36	55
Back-cross expected	46.75	46.75	46.75	46.75

On the other hand, the results in Mating *E*, a back-cross mating, are somewhat different from those reported by Dunn and Jull. The differences are best expressed in tabular form.

In the light of the results reported in this paper it now seems doubtful if there is linkage between rose comb and crest.

	R Cr	*r Cr*	*R cr*	*r cr*
Dunn and Jull.....	55	36	39	55
Jull (this paper)....	21	10	24	14
Total	76	46	63	69

Literature Cited

1. Bateson, W. 1909. Mendel's Principles of Heredity, Cambridge.
2. Bonhote, J. L. 1914. *Cairo Sci. Journ.* VIII, 83-90.
3. Cunningham, J. T. 1912. *Proc. Zool. Soc. Lond.* XVI, 241-259.
———. 1919. *Ibid.* XVI, 173-202.
4. Dunn, L. C. and Jull, M. A. 1927. On the Inheritance of some characters of the Silky Fowl. *Jour. Gen.* V. XIX, No. 1, pp. 27-63.
5. Punnett, R. C. 1923. Heredity in Poultry, London.

Agriculture on the Hypotenuse

TREE CROPS: A PERMANENT AGRICULTURE, *by* J. Russell Smith, Professor of Economic Geography, Columbia University. Pp. 333; 136 illustrations. Price $6.00. Harcourt, Brace and Company, New York. 1929.

At irregular and rare intervals books appear which, due to their subject matter or their style, depart widely from the current literature of their generation. *Tree Crops* is such a book. It is unique in both content and style. Its aim is to pioneer a new form of agronomic agriculture and thereby push into the remote future that gloomy day envisaged by followers of Malthus when the earth's population will require more food than can be produced. The preface is evidence regarding the unusual style of the book. It says:

> First, look at the pictures and the legends and you have the essence of it.
> Second, read the first three short chapters and you have the idea.
> Third, read the large print and you have the argument.
> Fourth, read the fine print and you have more details—of proof and application.

The theme of the book is that on steep lands the world over, tree crops, those producing food for men and animals, should be grown. To accomplish this, new and more valuable varieties of hundreds of species must be produced and their adaptations determined. It is realized that selection of the most valuable variants from among tree populations and their vegetative multiplication would bring only partial success. The plant breeder as well as the plant explorer must be enlisted in the crusade.

One would be inclined to believe that the author rather underestimates the difficulties, both biological and economic, of the plan which he proposes; if and when the world becomes hungry it may prove the pillar of fire leading to the land of plenty. It will arouse the interest and quicken the imagination of every intelligent reader. The number which it will move to action will be much smaller.

A new edition should be carefully examined to verify such statements as classifying Major Andre as a traitor (opposite page 4) and the suggestion that insects might improve the cross pollination of the pistache—page 230.

R. J. B.

MATRIMONIAL PROSPECTS OF SOUTHERN COLLEGE WOMEN

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ONE frequently sees in magazines and newspapers statements to the effect that about half the women who graduate from American colleges never marry; and the situation is generally viewed with alarm. There was a prolonged discussion of the question in the *Popular Science Monthly* between 1902 and 1905, soon after the census of 1900 showed a marked decrease in the size of American families in the preceding decade, and about the time that President Roosevelt raised the cry of "race suicide". The discussion has continued intermittently and with varying degrees of pessimism in other periodicals to the present day.*

Such statements seem to be based usually on the records of a few northern colleges, with no intimation that conditions might be different in different parts of the country. With a view of investigating the state of affairs in the South, the writer has made a study of the 1926 alumnae directories of the Georgia State College for Women (formerly Georgia Normal and Industrial College), at Milledgeville, and the Florida State College for Women, at Tallahassee, and the 1927 directory of Agnes Scott College (formerly Agnes Scott Institute), a Presbyterian school at Decatur, Ga., near Atlanta.

Sources of Data

The first graduates from the Georgia state institution were in 1892, but degrees do not seem to have been given there until 1921. In the alumnae directory the names are grouped by classes, and some of those receiving degrees since 1921 are listed as graduates a year or two earlier. For the sake of simplicity the graduates with degrees have been omitted from the present investigation, but it will be worth while to tabulate them a few years hence, when they are more numerous.

Agnes Scott College began as an institute in 1889 (first graduates 1893). It was raised to the rank of a college in 1906, and has given degrees since then. Its latest directory lists both graduates and non-graduates in an alphabetical list, and then groups the graduates (nearly 900 in number) also by classes. Those who attended but did not graduate are about twice as numerous, and their names appear in the alphabetical list only, with numerals indicating the classes to which they belonged, in most cases. (Where no class numerals are given the individuals are left out of these calculations.)

The Florida institution dates from 1905, and its degrees may be divided into three classes. First, L. I (Licentiate of Instruction), which is based on a short course, and probably corresponding to the graduates without degrees at the Georgia State College. Second, bachelors' degrees, and third, masters' degrees. The L. I. graduates, together with those who merely received certificates for special courses, and those whose degrees are not given in the directory, have been tabulated separately from the "bachelors"; but no study has been made of the masters' degrees, for they are too few for ac-

*One of the latest contributions to the subject is "Career or Maternity," by Henry R. Carey, in the *North American Review* for December, 1929. A more optimistic view is taken by Roswell H. Johnson, in *Eugenics* for September, 1929, who states that the percent married among graduates of Bryn Mawr, and the number of children per marriage, has increased in recent years, and the interval between graduation and marriage decreased. No explanation of the change is offered, but it may be due to a change in the kind of girls who go to college since the rapid increase in enrollment in nearly all colleges in recent years.

curate statistics, and practically all the holders thereof also have bachelors' degrees from the same institution. Quite a number have received the L. I. degree first and A.B. or B.S. a year or two later, and all such have been counted according to their latest status.

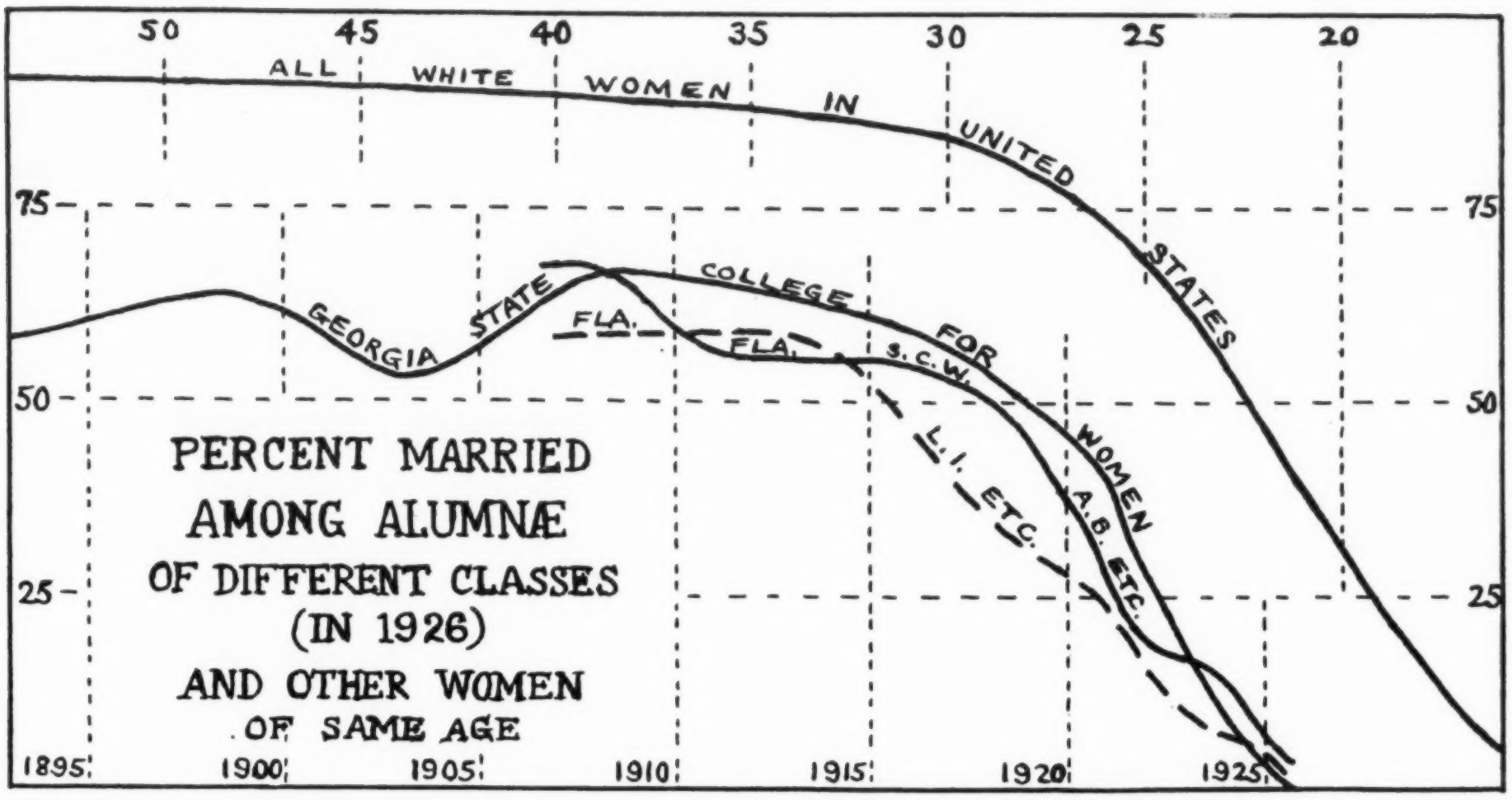
In the Florida directory all the names are put in a single alphabetical list, with degree, class, present address if known, and present name of those known to have been married. In several cases the year of graduation is not given; but most such cases with which the writer is personally acquainted are married women of mature years, who may have purposely withheld the dates; and for the present it is arbitrarily assumed that they all graduated in 1910 or earlier. There is a possibility of typographical errors in the dates when the names are not grouped by classes, but if such errors were at all numerous they would tend to balance each other to some extent. A few of the Florida alumnae (mostly wives of professors in the same institution) were evidently married before graduating or even before entering, but they have been counted the same as if they had married after graduation.

In all three directories some of the alumnae who are listed only by their maiden names, with no address, may really be married, for it is easy to lose track of a woman when she changes her name and address at the same time; so the percent married is probably a little larger than the records indicate; but such cases are probably not numerous enough to affect the validity of the statistics for comparative purposes. Neither directory tells anything about the date of marriage, the number of children, or whether an alumna has been widowed, divorced, or married more than once. Deceased alumnae are indicated, and they have been counted with the living ones; but if they had been excluded the proportion married would have been increased a little, because some who died young would doubtless have married if they had lived longer.

High Marriage-Rate of Agnes Scott Graduates

An article by one of the students, in the Sunday magazine section of the *Atlanta Journal* for Oct. 13, 1929, discussed the matrimonial situation at Agnes Scott, and pointed out that its alumnae showed a high marriage rate, for 61% of all the graduates, and 22% of those of the last six years, were already married. Of the 95 members of the class of 1929, 3 were married and 23 engaged at the time of graduation. It was further stated that only four of the whole body of alumnae were known to have been divorced; and the average age of marriage was said to be 25 years (this calculation based on unpublished data). The president was quoted as expressing the opinion that the presence of three men's colleges within a few miles (in Atlanta and suburbs) was a factor in the high marriage rate. (Similar statistics for co-educational colleges are not available at this writing.)

The accompanying graph (Figure 18) shows the percent married (including widows and divorcees, if any) among the graduates of the Georgia and Florida state institutions up to the latter part of 1926, for each class back to the beginning, except that the years previous to 1921 are averaged in five-year groups to make the curves smoother, on account of the comparatively small numbers involved in those earlier years. For the Florida college there are two curves, the continuous one for graduates with bachelors' degrees, and the broken one for L.I. degrees, certificates and unspecified. The high point at the beginning of the Florida A.B. curve is probably due largely to the arbitrary assumption previously mentioned, that the alumnae who did not give dates graduated in 1910 or earlier. If we had the exact facts that curve would probably lie between the two which it now crosses. The attendance at both institutions, as at nearly all other colleges, has increased rapidly in recent years; so that if a similar investigation should be made ten years from



MARRIAGE RATE OF GEORGIA-FLORIDA ALUMNAE

Figure 18

Graph showing percent married (including widowed and divorced) among all white women in the United States, at different ages (indicated by numbers at top) in 1920, and among graduates of the Georgia and Florida state colleges for women, of different years (indicated at bottom), according to their 1926 alumnae directories. Horizontal distances indicate years, and vertical distances percentages. The upper curve is fitted to the others on the assumption that the average age at graduation is about 21 years.

now, more accurate statistics could be computed.

There is added also a similar curve for all white women in the United States who are married, widowed or divorced, based on the census of 1920, and located with reference to the alumnae curves by assuming that the average at graduation is about 21. (If it should be found to be a little earlier or later than that, this upper curve would have to be shifted a little to the left or to the right.) As this curve is based on millions of individuals, it is much smoother than the alumnae curves, which are based on only a few hundred.

The Agnes Scott data are not plotted because they are for a period about a year later than the other two, and are therefore not strictly comparable; and also because the graph would be confusing if there were too many curves on it. But the proportion married among the graduates of Agnes Scott previous to 1916 is remarkably high, nearly 70%, while non-graduates for the same period averaged less than 60%. In the class of 1918, however, there were 70.2% married among the non-graduates and only 51.6% among the graduates; and the non-graduates have maintained the lead ever since. Evidently many girls left college prematurely in order to marry during the World War, which seems to have stimulated marriage in all ranks of society.* And since that time any cases of marriage before the completion of one's college course would naturally make the percent married higher among the non-graduates than among the graduates. The 1927 directory lists several married even among those who would have graduated in 1928 or 1929 if they had remained in college. But a decade from now more of those who graduated between 1917 and 1927 will

*The U. S. Census Bureau gathered no statistics of marriage between 1916 and 1922, but later estimated, from the returns of 25 states that kept such records, that the marriage rate in 1917 was 11.20 per thousand; a figure never exceeded except in 1920.

be married, and the shape of the curves for that period will be different.

Agnes Scott is said to have had a standard college curriculum ever since 1906, but the two state institutions named have gradually raised their curricula to the American standard in the last several years, and thus increased the average age of graduation, which complicates matters somewhat. For if a girl who stays in college until she is 20 years old thereby reduces her chances of marriage, a prolongation of the educational process for another year or two must still further reduce it.* All the college curves begin to bend downward at a point corresponding to about ten years before the date of the directories, and it is impossible to say just how much of that is due to raising the curriculum and how much to the shortness of the time elapsed since graduation. If no further change of academic standards takes place, similar curves constructed a decade later ought to show the effect of such changes in the past, if they are not masked by other factors. However, all the curves show graphically something that may be already fairly well known, namely, that nearly all marriages take place within ten years after graduation, and very few women of any sort marry for the first time after the age of 35.

All the curves for graduates of more than ten years' standing fluctuate around 60 per cent, as compared with 50 per cent which is about the average for northern colleges. This correlates fairly well with the easily demonstrated fact that both men and women marry earlier in the South than in the North; but it is quite possible that when the standard curriculum has had time to take effect in the institutions under consideration, their graduates will not differ much in this respect from the northern alumnae.

In the Florida statistics it will be noticed that the percent married is less (for most classes) among those who have taken a short course than among those who have bachelors' degrees. This at first would seem to contradict what has been said above; but there is a plausible explanation for the difference. Those who take only the L. I. degree presumably contemplate making teaching their life work, and they may have been born with less of that indefinable quality lately called "it" than those who go all the way through college while waiting for something romantic to turn up.

Marriage Rate of Ph.D.'s

But those who continue further and take masters' or higher degrees probably have much less chance of marriage than those who stop with the bachelors' degree. This cannot very well be shown by means of the Georgia and Florida alumnae lists, for the numbers are too small as yet, but it is clearly shown by a study of women scientists, based on the 1927 edition of Cattell's *American Men of Science*. In the first 135 pages of that work there are about 100 women, and only 17 per cent are obviously married, though the true number may be somewhat greater, for marital condition (and sometimes even the sex) is not always evident, being indicated only by the names. Most of the women scientists have doctors' degrees, and of those only 11.5 per cent seem to be married, as compared with 53.8 per cent of those who are not doctors.

All this, of course, does not neces-

*Some statistics from the Florida state census of 1925 throw a little light on this point. While directing that census the writer made a list of the students of the State College for Women, from the enrollment cards in the President's office, and found that the average age of all the students at the time of enumeration (February) was 19.9 years, while those from Tallahassee only, averaged 21.6 years. The most likely explanation of this difference is that the whole student body includes many girls from the rural districts, where men are in the majority, and it is customary to marry early; while Tallahassee is a city, with a considerable excess of women, and many Tallahassee girls were attending college who might have been already married if they had lived in a small town or in the country. It is very likely that the average age of students from other cities was similar to that for Tallahassee, but that point was not investigated.

sarily indicate that a college education reduces a woman's chances of marriage, for cause and effect are intricately involved. Some women (and men, too) are naturally more sentimental than others, and the less sentimental ones, who care less for matrimony, naturally gravitate toward an educational or business career, and that may be all there is to it.

Future editions of these alumnae catalogues could be made much more useful to students of social phenomena by the addition of some easily obtained information. The alphabetical arrangement used in Florida is the most convenient if one wishes to find a certain name quickly, but in other respects the Georgia method of grouping by classes seems preferable. (It would be better still to use both systems at the same time, as is done in the Agnes Scott directory and in the alumni catalogues of many men's colleges.)

Assuming the names to be grouped by classes, it would be desirable to give the following information about each alumna, each topic in a separate column if possible:

Name when in college.
Home when in college.
Year of marriage (if any).
Name of husband (if any) and year of his death if he is not living; or occupation if single or widowed.
Present address, or year of death if deceased.
Number of sons and daughters (using 0 for none and — for "no report").

The year of birth would also be of interest, but that would probably be asking too much; for many of the women in *Who's Who* do not give their ages. Some record should also be made of those who attended college but did not graduate, as is done by several state universities.

The "Fuchsia-Picture" of Mendel

The Cover

THE plaque reproduced on the cover is the work of Theodor Charlemont of Vienna. It is evidently based on the "Fuchsia-picture" of Mendel, believed to have been made between 1861 and 1864, but the flower has undergone rather extensive metamorphosis at the sculptor's hands. Even before his experiments with peas Mendel had crossed the fuchsia, and according to Iltis, a handsome double fuchsia was known for a long time in the trade as the "Mendel Fuchsia". Mendel later used this same flower on his abbot's escutcheon.

The signature below the picture was inscribed at the close of a brief autobiography included in an examination taken by Mendel at Vienna in 1850, to entitle him to a teacher's certificate in natural science. He did not pass the examination, nor a later one in 1856, but it has preserved to us interesting information as to Mendel's views on evolution, before the publication of the *Origin of Species*. It is curious that the other signatures given in Iltis' book are in German script, as is the text of this examination.

Charlemont also executed the statue of Mendel at Brunn, which was illustrated in the JOURNAL for November, 1925. The reproduction of the plaque is taken from *Gregor Johann Mendel*, by Hugo Iltis, Julius Springer, Berlin, 1924.

Photograph by David Fairchild

AVOCADO FLOWERS AT THE FIRST AND THE SECOND OPENING

Figure 19

The flower at the right is of the Grande variety at the second opening, showing the anthers open and the pollen masses exposed to insect visitation, with the stigma already discolored; on the left is a flower of the Winslowson variety open for the first time, with the stigma receptive, but not shedding pollen. The lower left flower is loosely closed with the spent anthers protruding. Magnified about five diameters.

POLLEN STERILITY IN THE COLLINSON AVOCADO

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In the course of pollination studies of the avocado (*Persea americana*) several rather unique floral adaptations have been found,* indicating cross pollination as the normal means of fruiting.

The avocado represents an extreme case of proterogyny in which not only is pollen shed from the individual flower after the stigma is (usually) past the receptive stage, but the two sets of flowers (receptive and pollen shedding) open and close synchronously so that there is scant (or no) opportunity for the stigma to receive pollen from a neighboring blossom on the same tree. Moreover, all trees of the same variety behave alike in this respect.

Two Types of Flower-Behavior

This synchronous opening and closing was first clearly demonstrated by Stout[4], and lead to a further discovery, viz: that avocado varieties could be divided into two groups, one group (Class A) having only "first-period" flowers (receptive) in the morning with "second-period" flowers (shedding pollen) in the afternoon; another group (Class B) shedding pollen in the morning from flowers open for the second time, with first-period flowers (receptive) in the afternoon. The flowers opening in the morning (whether in the first-period or in the pollen-shedding stage) usually close around noon, before the second set of flowers open for the afternoon period. (With a few varieties and under changing weather conditions there is occasional overlap permitting a certain amount of close pollination.

It was only by tagging large numbers of individual flowers and making hourly visits for several days at a time that this flower behavior was definitely established. It became clear that by interplanting varieties selected from these two classes, conditions would be favorable to securing cross-pollination, providing they bloomed at the same time and flying insects were present to carry pollen from tree to tree. While there are numerous instances in which self or close pollination is quite possible and good crops are thus secured, the agency of cross-pollination is a vital one with most varieties and is now given due consideration by most growers in planning their orchards.

The avocado flower on first opening presents an erect pistil with the stamens opened out in a nearly flat plane (see Figure 19.) No anthers are opened during this first period which lasts for three or four hours. On second opening the inner whorl of stamens, three in number, are folded in about the style. The anthers begin to open and dehisce within a half-hour to an hour, but the stigma by that time is usually brown and withered. The flowers that have their first opening in the morning (Class A) close around noon, and do not reopen and shed pollen until the following afternoon. The flowers that have their first opening in the afternoon (Class B) have a much shorter cycle. They close about dusk or earlier, and reopen the following morning, when their pollen is shed. In either instance the stigma rarely remains in receptive condition until pollen is shed, although flowers opening very late in the afternoon may sometimes carry their stigmas over night in good condition.

A curious anomaly was discovered by Stout and Savage[5] when studying

*See Literature Citations, 1, 2, 3, 4, and 5.

PROVING POLLEN STERILITY

Figure 20

Tree of Collinson Avocado selected for tenting experiment (left) and tented tree showing exposed branch. No fruit set on tented tree, while the exposed branch and other Collinson trees in the vicinity set fruit abundantly. Grove of J. W. Barney, Palma Sola, Florida.

the flower behavior of the Collinson variety. This variety originated at the United States Plant Introduction Garden, near Miami, Florida, as a seedling of the Collins variety, one of the Gautemalan race, and gives evidence of being a natural hybrid between the Collins and one of the West Indian varieties. It has the late maturing habit of the Guatemalan race with the smooth glossy green skin of the west Indian, and it is somewhat hardier than the West Indian type.

Examination of the flowers showed no abnormality, but repeated observations during the whole blossoming period revealed complete absence of pollen. The anther lids fail to open at any time during the flower cycle.

Notwithstanding this pollen sterility, trees of the Collinson variety are normally fruitful, but in every instance investigated by the writer, there occur trees of other varieties within a few rods that might serve as sources of pollen. Warning was promptly given to avocado growers[4, 5] against planting this variety without providing other trees (of Class B) as pollinators.

A Tenting Experiment

The regular fruiting of Collinson in South Florida had led to some skepticism among growers as to the necessity for cross-pollination, since in a few instances the opportunity for cross-pollination seemed rather restricted. Accordingly a tenting experiment was arranged during the spring of 1929 to test out this requirement. Tenting experiments had been made previously with varieties having normal pollen behavior[1, 3] both with and without bees as pollinating agents, the results showing the important rôle of these insects in the transfer of pollen. In this instance, however, the known absence of pollen made it desirable to test the pos-

sibility of fruiting without pollination, excluding all flying insects. Avocados are known in some instances to set fruit without pollination, but such fruit usually sheds at an early stage. Rarely a few unpollinated fruits remain to maturity but these fruits are practically always seedless, undersized and abnormal in shape. While flying insects were for the most part excluded by the tree tent, crawling insects such as ants and thrips were not excluded and the flowers were freely exposed to their visits. There is some reason to believe that the ubiqitous thrip, while in the main destructive, may serve occasionally in the transfer of pollen when probing normal avocado flowers.

This tenting experiment was carried out in a young avocado grove belonging to J. W. Barney, at Palma Sola, Fla. The orchard was originally planned to provide for cross-pollination and the Collinson trees each bore several fruits in their third year. Three reciprocating varieties (of class B) Winslowson, Queen and Panchoy are planted in close proximity, any one of which might have furnished pollen for fruit setting.

On February 18, 1929, before any open bloom appeared, a framework was built over one of the Collinson trees (No. 1) which was covered with "seedbed muslin", care being taken to leave no openings that would admit insects. The end of one of the lower branches was allowed to protrude from the tent, thus exposing the flowers to insect visitation (see Figure 20). On another tree (Tree No. 4) a single lower branch was similarly covered with muslin, leaving the main tree uncovered. Provision was made for opening these tents to permit inspection during the blooming period, but care was taken to admit no insects during inspection. On April 14 when blooming was nearly over, it was observed that, due to warping of one of the side cleats, a small opening had been made in one upper corner of Tent No. 1. One wasp and a few flies and gnats were inside the tent at this time. As in previous experiments examination of open flowers showed a complete absence of pollen although the flowers went through their cycle in a normal manner.

On April 22 blooming was completed and the tent covers removed. The foliage underneath the muslin cover was in good healthy condition and no defoliation or other apparent injury took place as a result of partial shade during bloom.

Inspection on April 14 showed no fruits set on tree No. 1 under the tent. Six tiny green floral ovaries of pinhead size were still adherent, but dropped within a few days. On the single branch exposed to insect visitation 38 fruits had set, from ¼ to ⅛ inches in diameter. On tree No. 4 the main tree had set fruit in abundance, with no fruit setting on the tented branch. A single branch comparable in size and position to the tented branch had set 21 fruits.

On April 22 (when the tents were removed, and blooming was at an end) the exposed branch of Tree No. 1 had 7 fruits holding, ¼ to ½ inches in diameter, with none on the main tree. This number of fruits (7) was more than such a small branch could carry to maturity and it was not surprising that on final inspection May 4, only one fruit remained, this one being on this date about one inch in diameter, and firmly attached. Tree No. 4 continued to carry a fairly heavy crop of fruit on the main tree, with no fruit showing on the covered branch.*

The results justify making special

*At the writer's suggestion a similar tenting experiment on a tree of the Collinson avocado was made by the late W. J. Krome at Homestead, Florida. This tree was tented March 16, 1929 and tent removed May 27, 1929; Mr. Krome's notes recently reported to the writer by Mrs. Krome read as follows: "We caged a Collinson tree under double wire netting, about the time bloom began to open and today removed this barrier to outside pollination (May 27). The shading due to the cage has left the tree in wonderful condition, but it is the only one in the entire row of Collinsons which is carrying no fruit at all.

provision for cross-pollination when planting the Collinson variety of avocado.

The satisfactory fruiting of this variety in mixed commercial plantings is corroborative evidence that cross-pollination is the usual method of fruiting with avocados generally, though with other varieties not absolutely obligatory. It is probably no mere accident that among all the avocado varieties investigated, approximately fifty per cent. fall into each of the two classes "A" and "B". In seedling groves, it has likewise been found by the writer that the number of morning and afternoon pollenizers is practically equal,—pollen periodicity being distributed among avocado seedlings much as the two sexes occur in seedlings of dioecious plants, such as the date palm.

Literature Cited

1. Clark, O. I. Avocado Pollination and Bees. *Calif. Avocado Assoc. Rpt.* 1922-3, pp. 57-62.

2. Nirody, B. S. Investigations in Avocado Breeding. *California Avocado Asso. Rpt.* 1921-22, pp. 65-78.

3. Robinson, T. Ralph and Savage, E. M. Pollination of the Avocado, *U. S. Dept. Agric. Circ.* 387. 1926.

4. Stout, A. B. A Study of the Cross-pollination of Avocados in Southern California. *Calif. Avocado Assoc. Rpt.* 1922-3, pp. 29-45.

5. Stout, A. B. and Savage, E. M. The Flower Behavior of Avocados with special reference to interplanting. *Proc. Fla. Hort. Soc.* 1925, pp. 80-89.

Books Received

BOOKS are acknowledged in this column as received, and such acknowledgment must be regarded as sufficient return for the courtesy of the sender. As far as space permits, books that contain material of special interest to the readers of the JOURNAL *will be reviewed in later numbers.*

New Views of Evolution, *by* George Perrigo Conger, Ph. D., Associate Professor of Philosophy, University of Minnesota. PP. 235. 10 Chapters. Price $2.50. Macmillan Company, New York, 1929.

A philosopher speaks on the evolution of evolutionary views, in Macmillan's "Philosophy for the Layman" series. We protest that the evolution of the horse and other organisms is different from the evolution of matter, and to try to squeeze both processes into the same shoe is hard on the layman.

Dust to Life, the Scientific Story of Creation, *by* Burton Peter Thom, M. D. Pp. 409. 12 Chapters. 120 Illustrations. Price, $5.00. E. P. Dutton & Co., New York, 1929.

Described on the jacket as a "Modern Genesis", it is also a Noah's Ark of pictures of animals that have lived on in stone. A brief glance raises a fear that the author has attempted to live up to the jacket and to speak with the "Tongues of Men and of Angels."

Process and Reality: An Essay in Cosmology. Gifford Lectures Delivered in the University of Edinburgh During the Session 1927-28. *By* Alfred North Whitehead, Fellow of Trinity College in the University of Cambridge, and Professor of Philosophy in Harvard University. Pp. 547. 5 Parts, 25 Chapters. Price, $4.50. Macmillan Company, New York, 1929.

If philosophical syntheses of current scientific concepts really do influence human behavior this should be a very important book.

ZUR ANTHROPOLOGIE DER MIKRONESISCHEN INSELGRUPPE KAPINGAMARANGI (Anthropology of the Greenwich Islands). by Otto Schlaginhaufen. Pp. 78. 4 Chapters. 10 Plates. Druck und Verlag Art. Institut Orell Fussli, Zurich. 1929.

Much data on hair, skin and eye characteristics, etc., etc., and many measurements and indices culled from the population of a tiny group of islands almost on the equator north of New Guinea. The data are topped off with an excellent series of plates showing how the Greenwich Islanders actually look when disentangled from the measurements and indices.

ABNORMALITIES IN PECANS*

I. Abnormalities in Pecan Flowers

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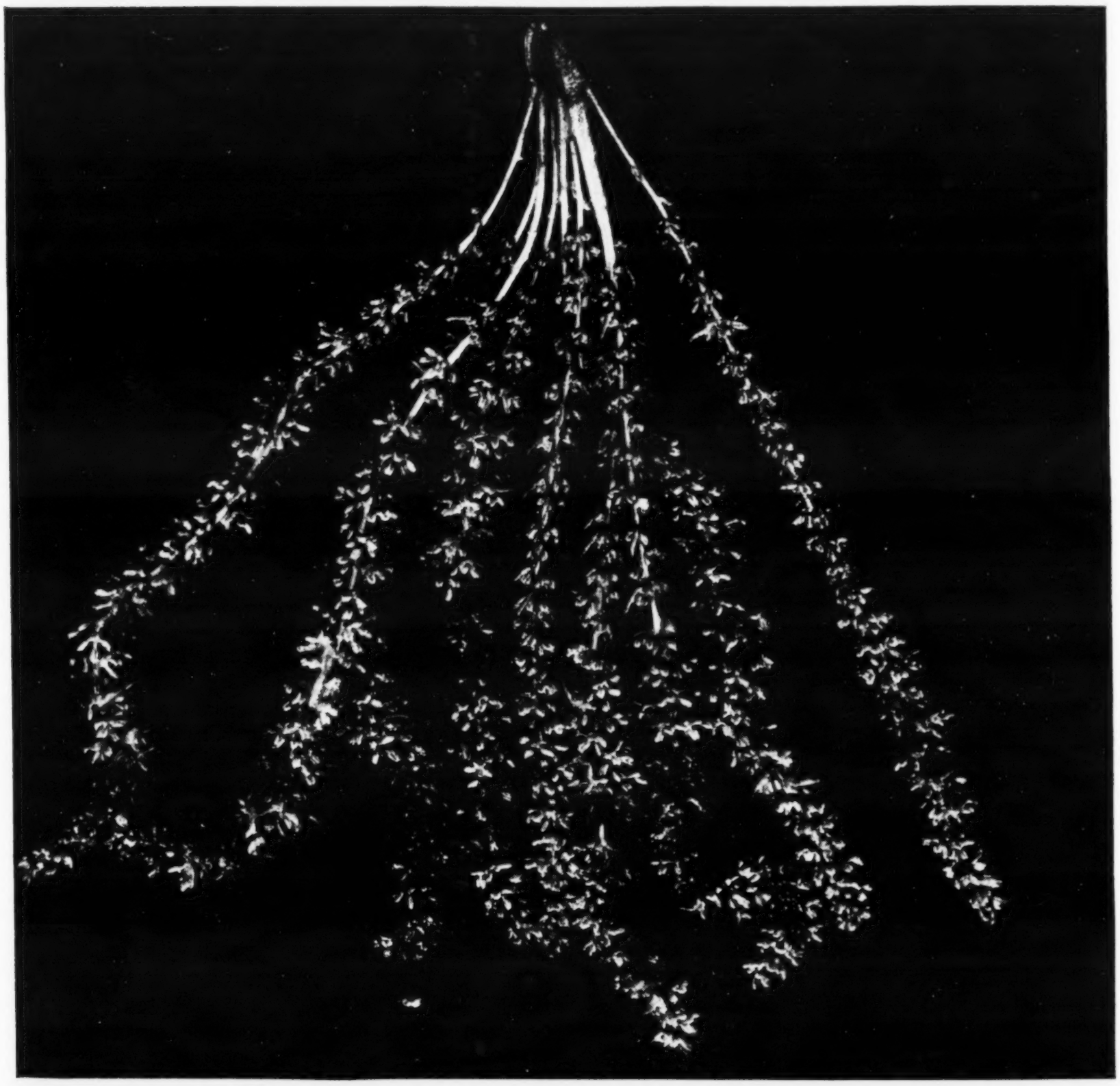


TRIPLETS IN PECAN CATKINS

Figure 21

A single cluster of the Jerome variety containing nine fully developed catkins (three times the normal number). This cluster was unfortunately infected with a fungus, *Microstroma juglandis* (Bereng.). Natural size.

WHILE studying the development of pecan flowers for the past seven years, the writers have examined many thousands of staminate and pistillate flowers of more than forty varieties of pecans in Georgia, Florida, Alabama and Mississippi. Variations with respect to color, size, form and time of initiation and development of pecan flowers considered normal for the particular variety have been described.[3,4,5] The aim was to record only normal behavior, leaving such abnormalities as were found undescribed.

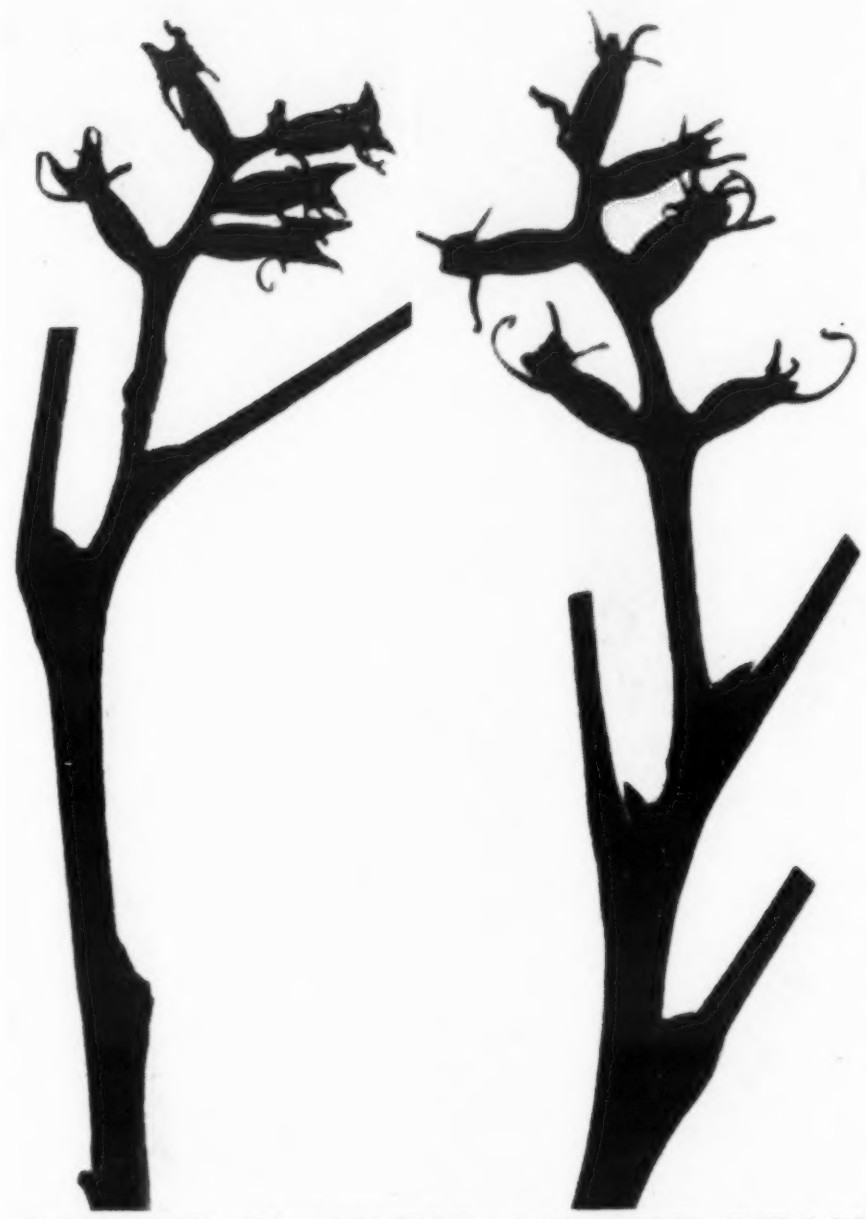
Normally the pecan (*Hicoria pecan* Brit.) is monoecious, the saminate flow-

*Published with the approval of the Director as Paper No. 32, Journal Series, Georgia Experiment Station.

"PERFECT FLOWER-CLUSTERS" IN THE PECAN

Figure 22

The cluster on the left has three normal pistillate flowers, and two catkins at the base of the cluster. The catkins were produced in the axils of the upper-most leaves. The cluster adjoining it has five normal pistillate flowers and three staminate flowers at the terminus of the cluster. The staminate flowers absciss immediately after dehiscence of the anthers. At the right is a group of four "perfect flower clusters" with from one to four pistillate flowers and from one to several staminate flowers borne at the terminus of the cluster. Such departures from the normal flowering habit are rare, but the fact that the same tree has been observed to produce these peculiar flowers for several years suggests that some of these variations, at least, have a genetic basis. (Slightly enlarged.)



FEMALE FLOWERS OF THE PECAN

Figure 23

Two normal groups of pistillate flowers of the pecan. (Natural size.)

ers (catkins) being borne laterally on "last year's" wood, and the pistillate flowers terminally, in clusters, on "current year's" wood. Two groups of three catkins each are produced at each node (Figures 24, 25). The pistillate flowers are borne in terminal spikes. From one to nine pistillate flowers, sessile, on a single axis, constitute a cluster (Figure 23). Abscission of the catkin group occurs immediately after pollen shedding.

The writers have observed four types of flower structure and arrangement considered abnormal.

"Perfect Flowers"

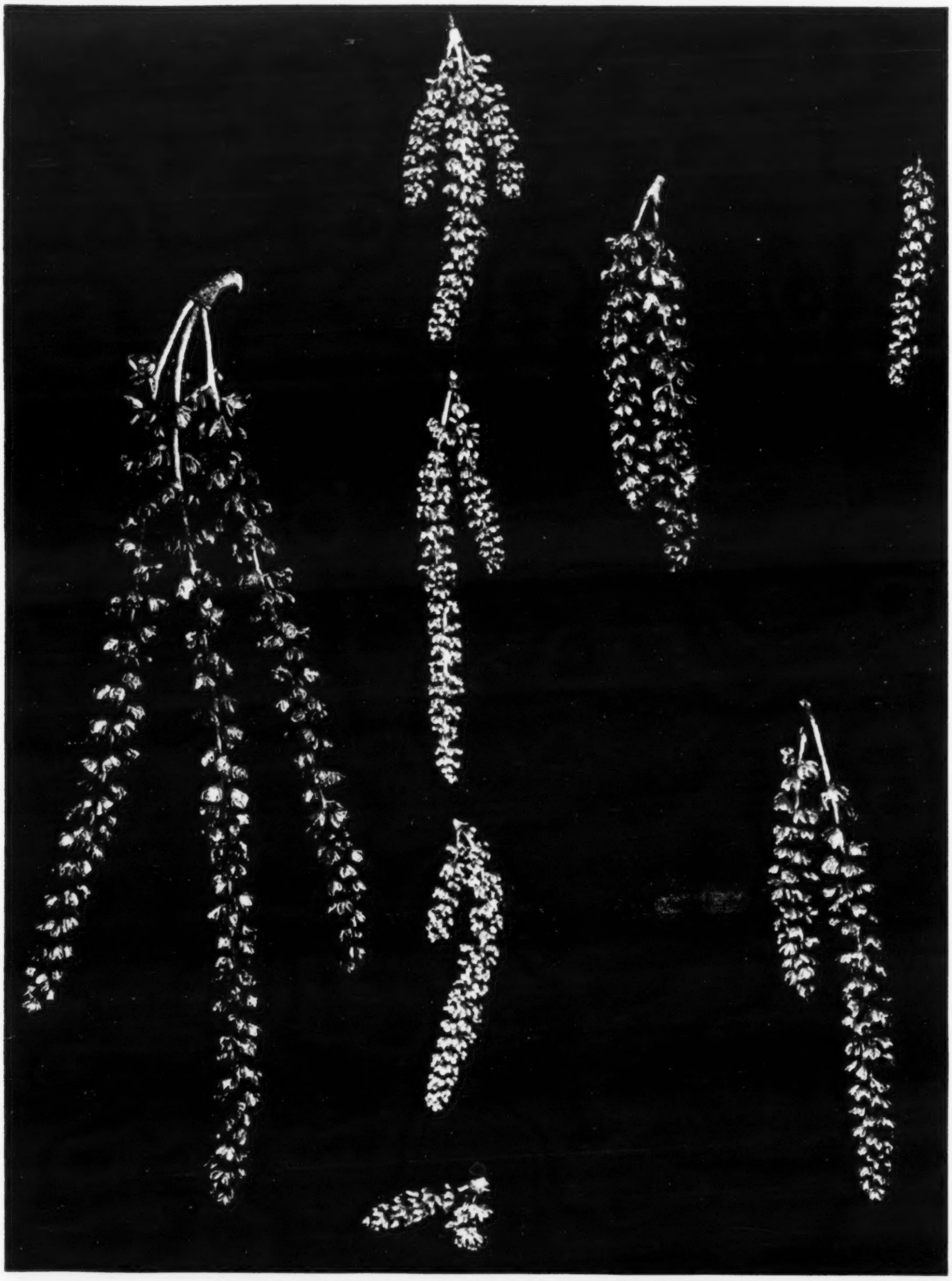
(A) For several successive years one tree of the Beveridge variety, growing at the Georgia Experiment Station, has produced "perfect flower-clusters" (Figure 22). A cluster of from one to five normal, pistillate flowers terminated the new spring growth, and at the terminus of the cluster of pistillate flowers was borne from one to several staminate flowers. A single axis, on current season's growth, produced staminate flowers capable of furnishing pollen and also pistillate flowers capable of receiving pollen. From five to forty per cent of the pistillate flower clusters of this tree have terminated with staminate flowers for three successive years.

The tree is twenty years old and has received the same care as thirty other varieties in the orchard. No other tree in the orchard has ever been known to produce such flower clusters. Thousands of trees throughout southeastern United States have been examined at blooming time and only one other tree has been found to produce "perfect flower-clusters." A Success tree at Ocean Springs, Mississippi, produced a very few such clusters in 1927. This tree has not been examined in other years.

The Success tree had received 400 pounds of a commercial fertilizer mixture in the spring of the same year, and it was thought that the peculiar floral structure might be related to high fertilization. Extremely heavy applications of commercial fertilizer and barnyard manure for two years have failed to produce "perfect flower-clusters" on trees of the Nelson and Teche varieties at the Georgia Experiment Station.

Microscopical examinations of the pistillate and staminate flowers of "perfect flower-clusters" have shown them to be normally developed though their arrangement differs markedly from the normal. When other conditions were normal[5] the pistillate flowers developed into mature nuts. In the case of the staminate flowers the bracts, anthers, and pollen were the same as those of normal catkins of the same variety. When the pollen was mounted in lactic acid and examined under high power, 63.4 per cent of the grains appeared normal. The anthers dehisced at about the same time as normal catkins on the same tree, and abscisson occurred immediately, or in some cases, abscission occurred without dehiscence.

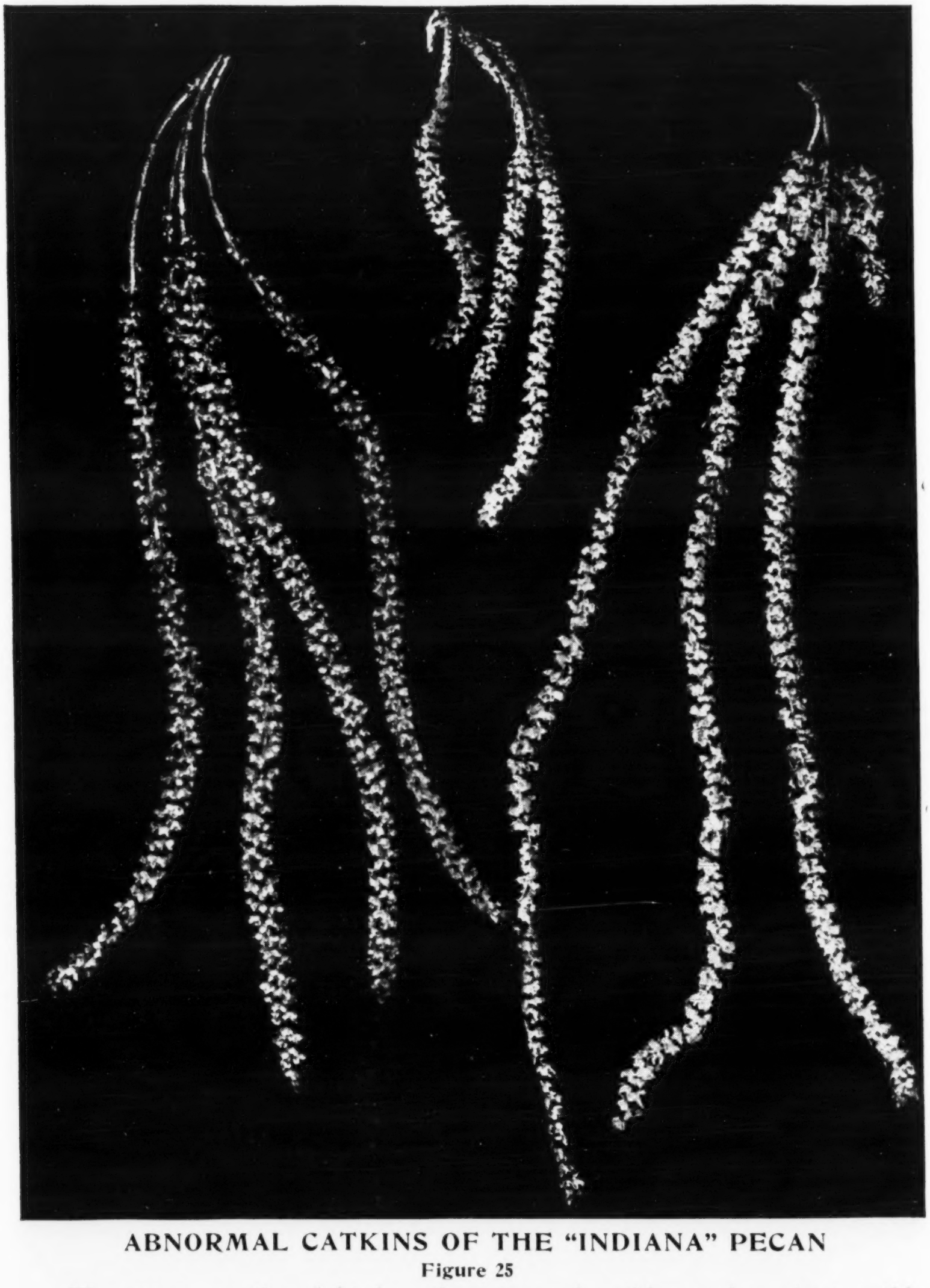
This phenomena is of little practical importance because cases are too rare,



CATKINS OF THE ALLEY PECAN

Figure 24

The group on the left is normal; the remaining seven groups show varying degrees of abortion. (Natural size.)



ABNORMAL CATKINS OF THE "INDIANA" PECAN

Figure 25

The group on the right has three normal catkins and a short catkin. The group on the left has four fully developed catkins; the small group at the top shows abortion of individual flowers.

and the amount of pollen produced is too small to be depended upon to affect pollination, as wind is the sole agent of dispersion.

(B) The second type of abnormality in pecan flowers is similar to the above except that staminate flowers are borne at the base of the flower cluster rather than at the terminus (Figure 22). A tree of the Jerome variety in the Experiment Station orchard is the only tree on which this has been observed. Both the staminate and the pistillate flowers of such clusters appeared normal and were capable of both producing and receiving pollen. The anthers dehisced and the catkin groups abscissed similarly to other staminate flowers on the same tree.

This phenomenon appeared to be the result of excessive stimulation in that one or more lateral buds on the "new wood" produced catkins. However, this was not observed on the Nelson and Teche trees when stimulated with commercial fertilizer and barnyard manure.

A behavior similar to this has been observed on trees of a number of varieties that were severely pruned in midsummer. Catkins which normally would come from lateral buds the following spring were "forced" out the fall before. Obviously, such behavior is a result of heavy pruning of the trees.

Variation in Number of Catkins

(C) A third type of abnormal behavior observed in pecan flowers is the occurrence of excess numbers of catkins in certain groups (Figures 21, 25). The Jerome and Indiana varieties, in 1928, produced groups of from four to nine catkins each, though not more than three catkins per group has been found on trees of any other variety Sometimes branching of the peduncle occurred near the base and at other times at various points along the catkin.

Behavior similar to the above has been reported by the writers, for the Nelson variety, and was shown in photomicrographs by Isbell[2] for the Earl variety; both of these being instances of groups of catkins in excess in a single bud, rather than catkins in excess in a single group.

No practical significance has been attached to this behavior because it has been observed only in years when there was an abundant crop of catkins on all parts of the tree. The number of groups on any tree to contain more than three catkins was not more than ten per cent of the total.

(D) A fourth type of abnormal behavior was the production of less than three catkins per group (Figure 24). Microscopical studies showed that the normal number of catkins was differentiated, but due to lack of vigor in the tree or in the twig or bud, abortion of one or more catkins occurred. The percentage of normal grains of pollen produced in catkins in which abortion occurred, was as high as the percentage of pollen produced in catkins in which no abortion occurred. Though the quantity of pollen produced in abortion cases is reduced by the reduction of the number of normal catkins, microscopical examination of the pollen showed that the quality was not reduced.

Summary

Wide experience in examining staminate and pistillate flowers of the pecan reveals four types of abnormal behavior, none of which are very prevalent nor of economical importance, but suggest that the flowering habit of the pecan is genetically unstable.

Literature Cited

1. Higgins, B. B. 1917. A disease of pecan catkins. *Phytopathology,* Vol. VII, No. 1, pp. 41-45. Illus.

2. Isbell, C. L. 1928. Growth studies of the pecan. *Ala. Agr. Exp. Sta. Bul. No.* 147. Illus.

3. Stuckey, H. P. 1916. The two groups of varieties of the *Hicoria pecan* and their relation to self sterility. *Ga. Agr. Exp. Sta. Bul. No.* 124. Illus.

4. Woodroof, J. G. and Woodroof, Naomi C. 1926. Fruit bud differentiation and subsequent development of flowers in *Hicoria pecan. Jour. Agr. Res.,* Vol. 33, No. 7, pp. 677-685. Illus.

5. ———— ———— and Bailey, J. E. 1928. Unfruitfulness of the pecan. *Ga. Agr. Exp. Sta. Bul. No.* 148. Illus.

HERITABLE CHARACTERS IN MAIZE

XXXIII. Slit Leaf Blade*

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SEVERAL small plants with longitudinal slits in the leaves were noted in a culture of maize which originated by selfing a flint corn collected by F. D. Richey and R. A. Emerson at Casilda, Argentina, South America. Certain of these plants were crossed with standard linkage testers. In the F_2 generation of these crosses the slit-leaved plants were found to segregate as a simple mendelian recessive. The character has been named slit blade, designated by the symbol *sb*.

Description of Slit Blade

The character slit blade is quite variable both in the time and degree of its expression. The longitudinal strips of tissues that first show evidence of change lie approximately midway between the main vascular bundles. Other mendelian characters are known in maize in which changes take place in this same region. Green stripe[2] and yellow stripe[1] may serve as examples. It has been pointed out[1] that the fact that the regions in which the change occurs are those farthest removed from the main channels of transport suggest that such changes are in some way causally related to the transport of materials to or from these regions.

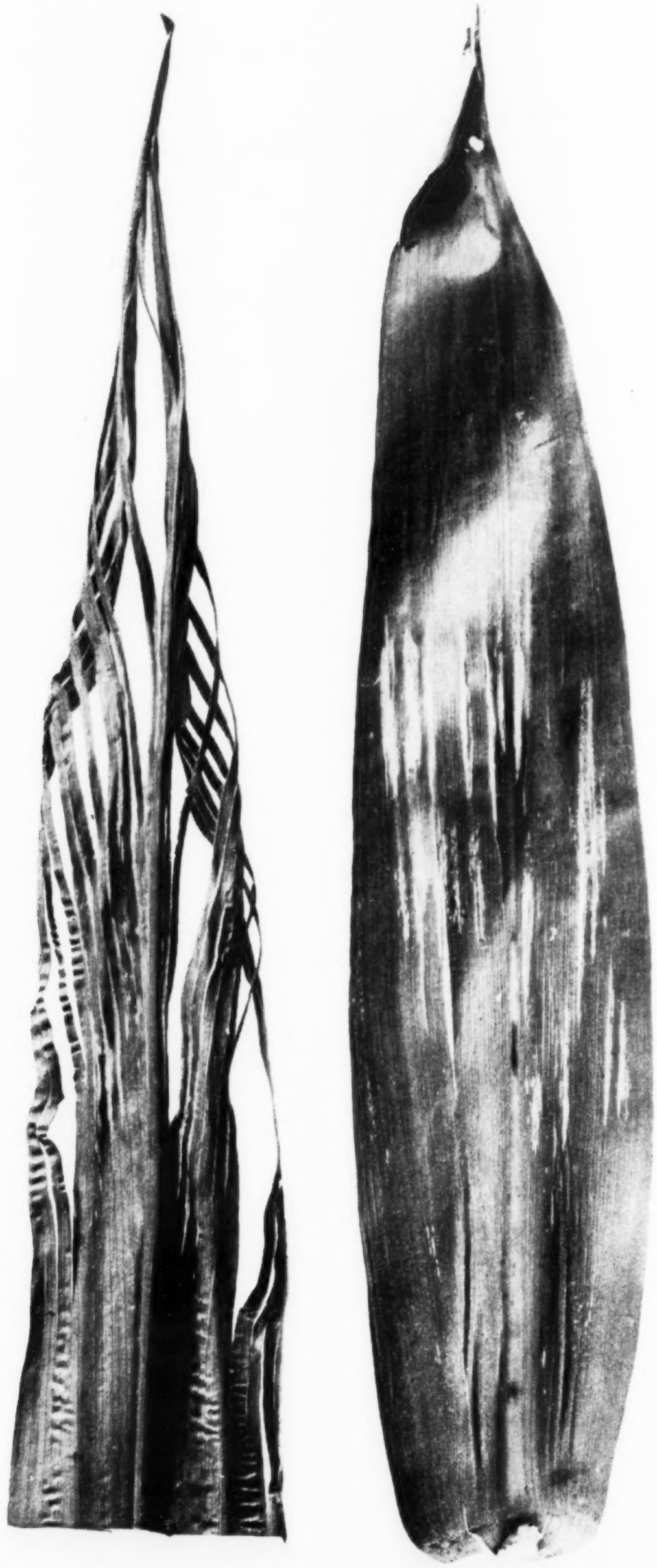
The characteristic slits in the leaf are produced by the mechanical tearing of the tissues along the weakened longitudinal regions. Few to many slits are produced during the course of development of slit plants. In Figure 26 are shown photographs of leaves from slit plants. The leaf shown on the left represents an extreme development of the character while the one shown on the right represents about the average condition of the leaves of slit-leaved segregates.

Slit plants are usually less vigorous than their normal sibs. In cultures in which the character develops early, the slit plants may be very weak, often not producing pollen or ears. In other cultures the slit plants may be difficult to distinguish from the normals. However, in most segregating cultures classification is rather easily made.

Studies of fixed and sectioned material have been made in order to determine the evident changes that take place during the disorganization of the cells in the regions affected by the gene for slit blades. The standard technic for sectioning in paraffin was used. Material of normal and slit sibs was sectioned and stained with Pianeze's stain. Duplicate material was stained with iron alum haematoxylin.

The first change noted in sectioned material of slit plants is a decrease in size of the plastids in the cells of regions affected. The plastids continue decreasing in size until they have completely disappeared. With the decrease in size of the plastids, a decrease in the amount of cytoplasm is noted. Soon after this the nucleus breaks down, leaving only the cell walls containing the remnants of the cell contents. The striae of dead tissue produced by this disintegration process are mechanically weak and are readily torn, producing the characteristic slits in the leaves. Figure 28 illustrates a transverse section through the leaf of a young slit plant. The region devoid of plastids was visible externally as an indistinct chlorophyll-free streak. Figure 27*A* illustrates a mesophyll cell from the leaf of a young normal plant. Figure 27*B* represents a cell from a slit sib of the same age. It is apparent that the number of plastids has been greatly reduced. The plastids remaining are much reduced in

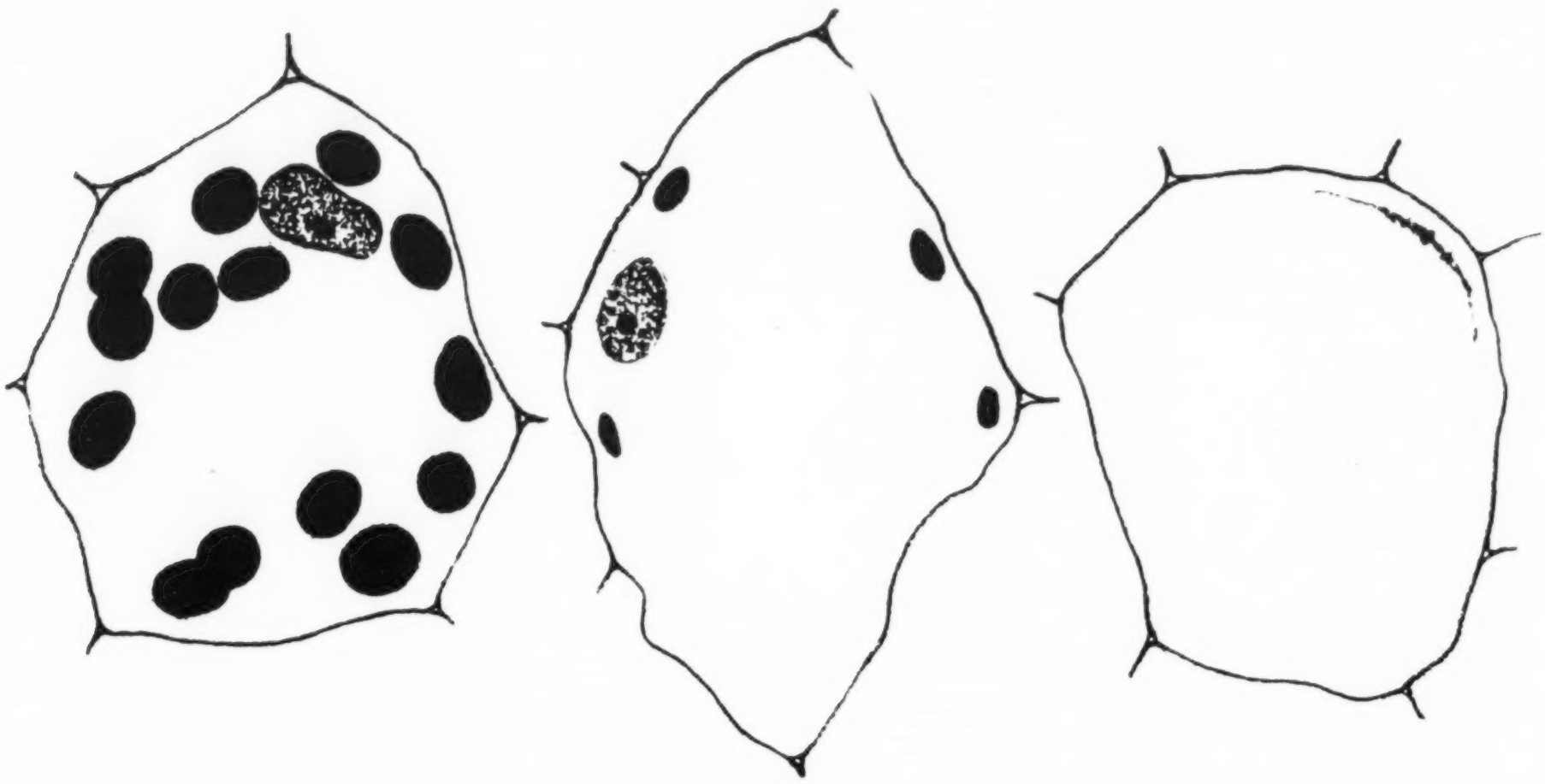
*Paper No. 168, Department of Plant Breeding, Cornell University, Ithaca, New York.



LEAVES FROM MATURE SLIT PLANTS

Figure 26

The left-hand leaf represents an extreme expression of the character; the hight-hand leaf more nearly the average.



PLASTIDS LACKING IN CELLS OF SLIT-LEAVED PLANTS

Figure 27

Illustrations of mesophyll cells from the leaves of young plants showing the normal condition (A), the decrease in number and size (B) and the ultimate disappearance (C) of plastids in slit-leaved plants.

PLASTID-FREE CELLS

Figure 28

Photo-micrograph of a transverse section through the leaf of a young slit plant showing the disappearance of plastids in the region affected by the slit blade gene. Photograph by M. Gordon.

size. Figure *27C* shows a cell almost completely disintegrated. Only a small remnant of the cell contents remains.

Linkage Relations of the *sb* Factor

Counts on cultures segregating for the slit blade gene and standard linkage tester characters show that the slit blade factor is located in the *Y-Pl* linkage group. A summary of available data involving *sb* and other factors in the *Y-Pl* group is given in Table I. The first indication of linkage of the slit blade gene was with a factor for male sterility. The data enable one to calculate a recombination value of about 10 per cent for these two genes. It was later found that the male-sterile gene involved was rather closely linked with the *Y* factor for endosperm color. Data obtained were in the repulsion phase and do not enable one to calculate accurately a recombination value. Using the coefficient of association as a means of calculating recombination percentage, one obtains a value of 19 per cent. Jones[3] has data showing a very close linkage between a male-sterile factor and the *Y* factor. It seems probable that the male-sterile involved in the material under discussion might be genetically similar to the one shown by Jones to be linked with *Y*. The genetic relations between these two factors for male sterility are being tested.

The *Y* factor and *sb* appear to be more loosely linked than *sb* and the male-sterile factor concerned. A calculation from repulsion F_2 data gives a recombination value of about 38 per cent. The data involving *Y* and *sb* are not entirely satisfactory. As is often the case with recessive factors, *sb* is deficient. Backcross data involving *Pl* and *sb* in the coupling phase are available. These data suggest that the two genes involved are inherited independently. This is to be expected if the order of the genes is *sb-Y-Pl*.

Data arranged so as to enable one to compare the linkage intensity between *Y* and *Pl* and that between *ms* and *Pl* are inconsistent and do not enable one to determine the order of these genes.

The available data as summarized in Table I suggest that the order of the genes involved is *sb-ms-Y-Pl*.

Summary

A recessive factor in maize called slit blade, with the symbol *sb* is described.

It is shown that slit blade is characterized by a decrease in size and ultimate disappearance of the plastids in certain longitudinal regions between the main vascular bundles of the leaf. Nuclear disintegration follows and the tissues made up of the dead cells are often mechanically torn.

The *sb* gene lies in the *Y-Pl* chromosome, some distance to the left of *Y*. The order of the genes is *sb-Y-Pl*.

Literature Citetd

1. Beadle, G. W. Yellow stripe—a factor for chlorophyll deficiency in maize located in the *Pr pr* chromosome. *Amer. Nat.* 63:189-192. 1929.
2. Emerson, R. A. The inheritance of certain forms of chlorophyll reduction in corn leaves. *Twenty-fifth Ann. Rept. of the Nebr. Agr. Exp. Sta.* 89-105. 1912.
3. Jones, D. F. Unpublished data.

TABLE I— Data Showing the Linkage Relations of the Character Slit Blade

Genes*		Pollination and linkage phase	Number of individuals					Percentage of total		Percentage recombinations**
X	Y		X Y	X y	x Y	x y	Total	x	y	
Ms	Sb	Self Coupling	530	21	54	136	741	25.6	21.2	10
Y	Ms	Self Repulsion	323	137	120	4	584	21.2	24.1	19
Y	Sb	Self Repulsion	347	99	114	14	574	22.3	19.7	38
Pl	Sb	Backcross Coup.	91	76	76	65	308	45.8	45.8	49
Pl	Ms	$\frac{Pl\ Ms}{pl\ ms} \times \frac{pl\ Ms}{pl\ ms}$	66	8	66	26	166	55.4	20.5	29
		Self Coupling	127	36	32	20	215	24.2	26.0	39
Y	Pl	$\frac{Y\ pl}{y\ Pl} \times \frac{Y\ pl}{y\ pl}$	48	77	26	15	166	24.7	55.4	31
		Self Repulsion	117	52	45	1	215	21.4	24.7	15

* X and Y represent the dominant allelomorphs of the genes listed in columns 1 and 2, respectively, while x and y represent their corresponding recessive allelomorphs.

** Percentage recombinations calculated by means of the coefficient of association and given to the nearest whole number.